A REVIEW OF THE NORTH AMERICAN FOSSIL AMIID FISHES

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CONTENTS

Abstract. North American amiid fishes range from Cretaceous (Albian) to Recent. Amiids are common fossils in Late Cretaceous and Tertiary freshwater deposits and apparently occupied a habitat much like that of the Recent species *Amia calva*. Morphometric, meristic, and cranial characters of articulated specimens from the Fort Union Formation (Paleocene), Green River Formation (Eocene), Florissant Formation (Oligocene), Pawnee Creek Formation (Miocene), and a Recent *A. calva* sample from Wisconsin have been used here in an attempt to revise the taxonomy and evolutionary history of the group.

Whereas seven genera and twenty-three species of fossil amiids have been described on the basis of disarticulated, often isolated elements, only three taxa have been described from complete or partially complete material. *Amia fragosa* (Late Cretaceous to Middle Eocene), *A. uintaensis* (Paleocene to Early Oligocene), *A. scutata* (Early to Middle Oligocene), and *A. calva* (Middle Pliocene to Recent) are here considered the only valid taxa. Amiid remains are first known in the North American fossil record from the Early Cretaceous (Albian) Paluxy Formation of Texas. This disarticulated material shows resemblances both to *Amia* and to the Late Mesozoic European genera *Urocles* and *Amiopsis*. *Paramiatus gurleyi* (Romer and Fryxell, 1928) from the Green River Formation of Wyoming is a synonym of *A. fragosa*. The differences between *Amia* and the large Early Cenozoic form *Protamia* are insufficient for recognition of *Protamia* as a genus distinct from *Amia*. The Eocene and Oligocene forms *Protamia media, Pappichthys medius, P. plicatus, P. sclerops, P. laevis, P. symphysis, P. corsonii, Amia whiteavesiana,* and *A. macrospondyla* are synonyms of *A. uintaensis;* they were based on undiagnostic cranial and vertebral characters. Morphometric and meristic similarities indicate that little evidence exists for maintaining separate Oligocene species *Amia scutata* and *A. dictyocephala*. *Amia exilis* is a synonym of *Amia scutata;* it was based on undiagnostic vertebral characters. *A. scutata* is morphometrically distinguishable from *A. calva* only on the basis of a slightly larger head/stan-

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dard-length ratio. The Eocene taxa *Amia depressus, A. newberrianus, A. gracilis,* and *Hypamia elegans* are *nomina dubia.*

Comparison of the fossil forms with the Recent *Amia calva* suggests the following taxonomic and possible phylogenetic relationships: (1) *Amia fragosa* survived until the Middle or Late Eocene, with no phylogenetic affinities with the modern form; (2) *Amia uintaensis* appears to be closer than *Amia fragosa* to the ancestry of *Amia calva,* which evolved through an intermediate form such as *Amia scutata;* (3) establishment of the Recent species *Amia calva* had begun at least by the beginning of the Pliocene; and (4) there are similarities in the Paleocene and Eocene amiid fossil record of North America and Europe.

INTRODUCTION

Amia is a genus of freshwater fishes that includes one of two extant representatives of the holostean level of organization. It includes a number of species of which only *Amia calva* exists today; other forms of *Amia* are found in the fossil record, and extend from the Late Cretaceous to approximately the Middle Pliocene. This study is an attempt to determine the taxonomic and phylogenetic relationships among the various species of *Amia.* It is established on osteology as well as on morphometric and meristic data from both Recent and fossil forms. This data is used to compare the available features of the fossil forms with Recent *Amia calva* and to determine the validity of previous descriptions based on various osteological, morphometric, or meristic character-states.

Until recently, a major difficulty in interpreting the taxonomy of fossil amiids has been the paucity of articulated specimens. Five genera and twenty-one species of fossil forms have been described from disarticulated, often isolated, elements (Table 19); only two taxa have been described from articulated specimens: *Paramiatus gurleyi* (Romer and Fryxell, 1928) and *Amia scutata* (Osborn *et al.,* 1875). Recent works by Estes (1964) and Estes and Berberian (1969), based on disarticulated elements from the Late Cretaceous Lance and Hell Creek formations, are the only published studies of *Amia fragosa,* although O'Brien (1969) completed an M.A. thesis on the osteology of *A. fragosa,* describing articulated specimens from the Late Cretaceous Edmonton Formation of Alberta.

Much more articulated material is now available and provides more detailed information on the cranial and postcranial anatomy of amiids. These specimens have been useful in this revision of the taxonomy as well as in the determination of possible relationships to European and Asian forms.

In an attempt to understand the evolution and interrelationships of the fossil and Recent amiids, a growth-series study has been made on a Recent *A. calva* sample from Wisconsin, and is compared morphometrically and meristically with the fossil forms. A great number of fossil specimens, including the holotypes and paratypes of all North American amiid species, have been examined. Several European taxa have been studied at the British Museum (Natural History), London; Muséum National d'Histoire Naturelle, Paris; and the Institut Royal des Sciences de Belgique, Brussels.

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ABBREVIATIONS

AMNH—American Museum of Natural History, New York, New York.
ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania.
BMNH—British Museum (Natural History), London, England.
CM—Carnegie Museum, Pittsburgh, Pennsylvania.
F:AM—Frick-American Museum Collection, New York, New York.
FHKSM—Fort Hays Kansas State Museum, Hays, Kansas.
FMNH—Field Museum of Natural History, Chicago, Illinois.
FSM—Florida State Museum, Gainesville, Florida.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
MNHN—Muséum National d'Histoire Naturelle, Paris, France.
NMC—National Museum of Canada, Ottawa, Canada.
PU—Museum of Natural History, Princeton University, Princeton, New Jersey.
ROM—Royal Ontario Museum, Toronto, Canada.
SMUSMP—Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas.
UA—University of Alberta Museum, Edmonton, Canada.
UCMP—Museum of Paleontology, University of California, Berkeley, California.
UMM—West Texas Museum, University of Texas, El Paso, Texas.
UMMP—University of Michigan Museum of Paleontology, Ann Arbor, Michigan.
UMMZ—University of Michigan Museum of Zoology, Ann Arbor, Michigan.
USNM—National Museum of Natural History, Washington, D.C.
YPM—Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

AMIA CALVA LINNAEUS, 1766

Amia calva is the only extant species of the family Amiidae. It is a predaceous fish that exclusively inhabits fresh waters of the eastern United States. Except for the gar, *Lepisosteus*, *Amia calva* is the only other living representative of the holostean fishes. Its common name, "bowfin," refers to the long dorsal fin that arches in a bow over most of the length of the fish's back. *Amia calva* has previously been known as the dogfish, marshfish, mudfish, grindle, or lawyer.

The osteology of *Amia calva* has been extensively described and discussed by Schufeldt (1885), Bridge (1877), Allis (1889, 1897), and Goodrich (1930). The following discussion is limited only to the nomenclatural problems, ecology, geographic distribution, and character-states of *Amia calva* that are relevant to study of the fossil forms.

Nomenclature

Jordan and Evermann (1896) noted that although Linnaeus (1766) had applied the binomial name *Amia calva* to the genus, Gronow (1763) had earlier used *Amia* as a nonbinomial name for fishes presently classified as *Apogon* Lacépède. They further suggested that should Gronow's earlier application of the name be given precedence and transferred to *Apogon*, then *Amiatus* Rafinesque (1815) should replace *Amia* Linnaeus. Jordon (1906) stated that this transfer of names was a necessary compliance with the rules of nomenclature, but later (1919), although citing Opinion 20

(1910) of the International Commission on Zoological Nomenclature which favored Gronow's priority, Jordan found the transfer of names inconvenient, for most authors had rejected Gronow's names as pre-Linnaean. In 1925, Jordan recommended to the Commission that certain names of Gronow supported by Opinion 20 be rejected in favor of the more accepted Linnaean terminology. The Commission's Opinion 89 (1925) resolved (among others) the nomenclatural problem of *Amia,* by concurring with Jordan's recommendation that ". . . *Amia* Gronow be set aside in favor of *Amia* Linnaeus, even if other names of Gronow are allowed." Rafinesque's name *Amiatus* is then a junior synonym of *Amia* Linnaeus.

Some later workers seem to have been unaware of Opinion 89. Thus Hussakof (1932) accepted the validity of the transfer of the name *Amia* Gronow to the percoid teleost *Apogon.* Romer and Fryxell (1928) named their fossil amiid from the Eocene Green River Formation *Paramiatus* instead of *Paramia,* and Whitley (1954) changed the name of Lehman's (1951) fossil amiid from the Eocene of Spitzbergen from *Pseudamia* to *Pseudamiatus.* The latter is invalid as *Pseudamia* was a valid name in itself and *Pseudamiatus* is its junior synonym regardless of the *Amia-Amiatus* controversy.

Ecology

Aside from notes regarding breeding, diet, and zoogeographical occurrences, little has been written in the past 50 years about the ecology of *Amia calva.* Dean (1898) and Reighard (1903) have made the only extensive published investigations of the habits and habitat of the fish. A thorough study of the biology of *A. calva* throughout its range is long overdue.

Geographic Distribution

The distributional map of *Amia calva* (Fig. 1) is based on information drawn from Hubbs and Lagler (1967), and Blair *et al.* (1968), and from examinations of unpublished records at the Ohio State University Museum of Zoology, Museum of Comparative Zoology, and the University of Michigan Museum of Zoology. The distribution limit is a flexible boundary allowing for seasonal occurrences and other natural variations. The known northern limit of *A. calva* extends from the Mississippi drainage system in Minnesota south of Duluth, eastward through Lake Nipissing and the Ottawa River to the St. Lawrence-Champlain basin (encompassing Quebec as far north as Quebec City, and Vermont). *A. calva* is distributed throughout the Great Lakes region, but is not found in the Lake Superior drainage basin, except in its outlet, the St. Mary's River. Southward, it has been recorded from the Hudson River to western Connecticut (recorded as the result of introduction; Hubbs and Lagler, 1967); Harrisburg, Pennsylvania, to the Susquehanna River; and along the Atlantic slope to the Carolinas and Florida. Westward, *A. calva* occurs along the Gulf Coast to southern Texas as far south as Brownsville, and northward, through eastern Texas, southeastern Oklahoma, northwestern Arkansas, eastern Missouri, and approximately 50 miles west of the Mississippi River to Brainard, Minnesota.

Pleistocene Occurrences

Amia calva has been reported from only three Pleistocene localities: (1) Chicago, Illinois, (2) Vero Beach, Florida, and (3) Itchtucknee River deposits, Columbia County, Florida (MCZ 9524, 9529, 9542). Hay (1911: 552) reported "Professor Frank Baker (Chicago Academy of Science) has shown me a considerable part of the skeleton and scales of a bowfin which he found in the Pleistocene clay near Chicago." A thorough search of the Chicago Academy of Science collections failed to produce this specimen. Hay (1917, 1923) listed *Amia calva* among the fossil vertebrate remains found in the Pleistocene sands at Vero Beach, Florida. Swift (1968), in his review of fossil fishes of Florida, figured Hay's *Amia* specimens (left dentary and a gular plate; FSM collections) and concluded that

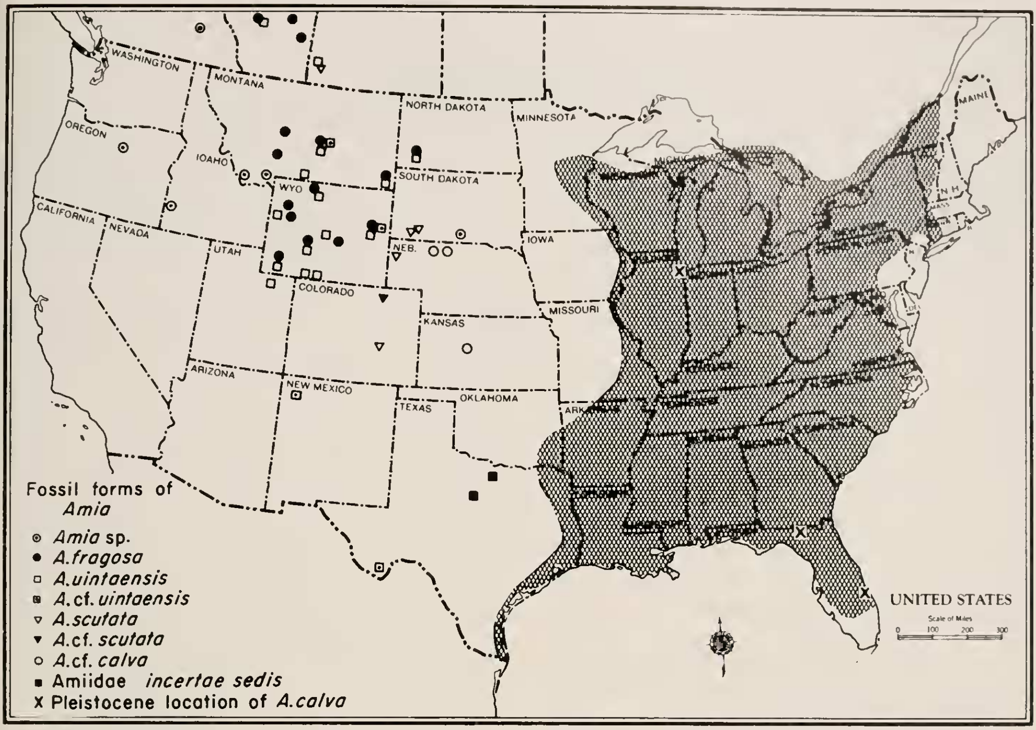


Fig. 1. Distribution of *Amia calva*. Fossil occurrences of *Amia* spp. are represented by symbols explained in the legend.

A. calva was probably very common in the Pleistocene fresh waters of the United States. The paucity of Pleistocene material does not necessarily mean the fish was not common in the Pleistocene, but does indicate that *Amia* remains have not been extensively collected or identified in existing museum Pleistocene collections.

Diagnosis

Vertebral meristics similar to *A. scutata*, but head/standard-length proportion (0.271 mean) is smaller than in the fossil forms. Extrascapular strap-shaped and relatively wide at midline, as in *A. scutata*, but posterior edge is curved so that it is proximally convex, then concave toward the distal corner, which results in a posterolateral projection. Pterotic borders frontal posteriorly rather than laterally; anterior end is as wide as posterior end. Orbital excavation is shallower than in other species, with a mean depth-to-length ratio of 0.100. Infraorbital 4 is smaller than infraorbital 5, less robust than in fossil *Amia*. Preoperculum as wide dorsally as ventrally. Symphyseal incurving of dentary relatively less than in *A. fragosa*, but greater than in *A. scutata* and *A. uintaensis;* little or no overlapping of dorsal coronoid articulation surface on ventral surface of ramus; deep Meckelian groove. Ventroposterior process of cleithrum less sculptured than in other species of *Amia*. Vomerine teeth sharp, conical, numbering between 15–27, more anteriorly placed than in *A. uintaensis* or *A. fragosa*. Bones less ossified than in fossil *Amia*. Greatest known standard-length 650 mm.

MORPHOMETRICS

Comparison of morphometric and meristic data of Recent and fossil *Amia* has facilitated an evaluation of the taxonomy as well as clarified anatomical trends. Many generic or specific character-states for *Amia "dictyocephala," Amia scutata, "Paramiatus gurleyi,"* and *Amia fragosa* have been previously established on osteological data based primarily on gross anatomical proportions (head/standard-length ratio and positions of insertion of pelvic and anal fins/standard-length ratios) and skull proportions (parietal/frontal and operculum width/length ratios). Meristic character-states have also been used for *A. "dictyocephala"* and *A. scutata.*

Although an age-growth analysis on *Amia calva* was done by Cartier and Magnin (1967), no morphometric investigation of a growth-series of Recent *A. calva* has yet been completed or used for comparison with fossil forms. Estes and Berberian (1969: 10) suggest that knowledge of the growth-series of *A. calva* would be of considerable importance in tracing the ancestry of the modern species.

Hammett and Hammett (1939) made a morphometric study of the Recent *Lepisosteus platyrhincus,* taking length dimensions of a sample of live fish from Florida. Since *Lepisosteus,* like *Amia,* is one of the two extant holosteans, their analysis is potentially useful in providing information on the ancient species. However, they did not actually compare the live material or data with any fossil material.

According to Imbrie (1956), Simpson *et al.* (1960), and Gould (1966), growth studies offer excellent means with which to clarify evolutionary and taxonomic problems in the fossil record. An interesting model utilizing morphometric data for synonymy of fossil forms was made by Thomson and Hahn (1968) on the growth-series patterns of Devonian rhipidistian fishes, in which they showed that *Thursius clappi* was actually a juvenile form of *Eusthenopteron foordi.* In studying fossil material, as Thomson and Hahn (1968: 201) indicate, there is a problem in determining the age, sexual maturity, and environmental regime of the animal. Also, of course, it is necessary to have sufficient fossil material with which to erect an adequate growth-series.

This present analysis is undertaken (1) to determine whether skull and axial skeletal proportions of amiids are isometric or allometric with increasing size, (2) to establish the variation in meristic characters of Recent *A. calva,* and (3) to compare morphometrics and meristics of Recent *A. calva* with those of the fossil forms. This study utilizes a small sample of 18 Recent *A. calva* specimens from the St. Croix River, Wisconsin. Measurements were taken from a growth series that includes the size range of most of the articulated fossil forms. The largest *A. calva* specimen, from St. Joseph County, Michigan (UMMZ 197683), was analyzed to see whether the large specimen would agree with the anatomical proportions and meristic characters of the Wisconsin specimens. Three smaller specimens from Pewaukee, Wisconsin (MCZ 8970), were also included. The fossil sample contains six complete and ten partially complete amiid specimens ranging in age from Late Cretaceous to Late Miocene which, although morphometrically similar in varying degree, are too few to warrant conclusions in themselves.

Methods

Measurements chosen for this study (Fig. 2) are those of Hubbs and Lagler (1967: 20). In fossil forms, because of the lack of preservation of internal soft anatomy as well as the impossibility of determining their interbreeding potential, these particular measurements necessarily assume an increased taxonomic significance, since they often provide the only viable parameters with which to designate genera and species. Measurements taken on *A. calva* are limited to those also represented in the fossil specimens. Each of the *A. calva* measured was X-rayed, except for three small specimens, which were cleared and stained. The range of error for all measurements taken on Recent and fossil material is ±0.04 mm. The range of error for the ratios is ±0.08 mm;

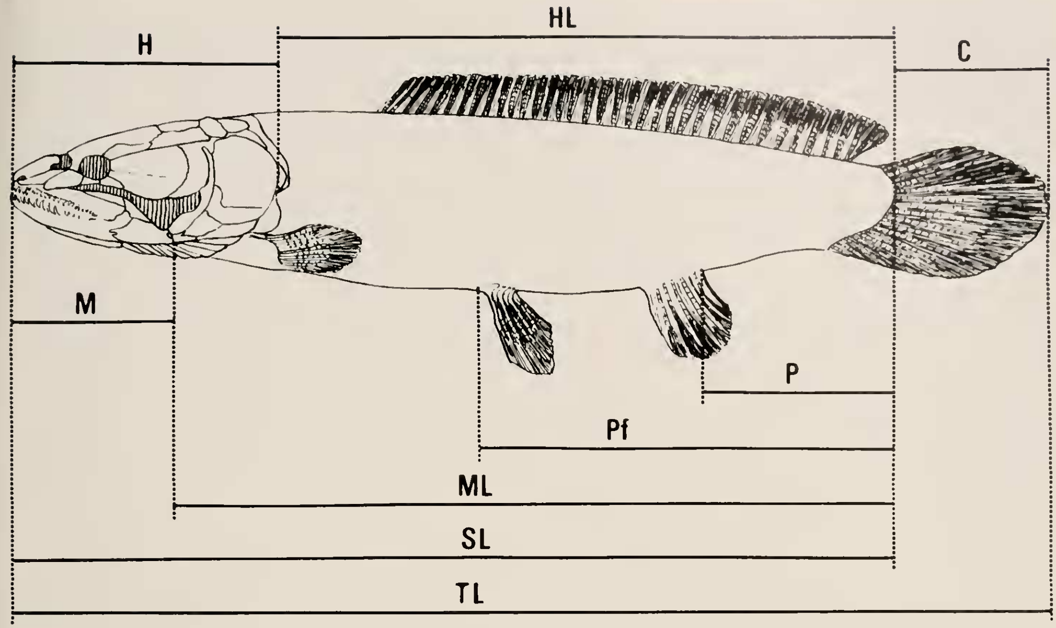


Fig. 2. Index to the measurements used, superimposed upon an outline drawing of *Amia*.

Key for body measurements:

TL = Total-Length
SL = Standard-Length
H = Head-Length
C = Caudal-Length
Pf = Insertion of Pelvic Fin
P = Insertion of Anal Fin
HL = Standard-Length minus Head-Length
ML = Standard-Length minus Mandible-Length

Key for abbreviations of cranial elements used in morphometric study:

M = Mandible
G = Gular
I^5 = Infraorbital 5
F = Frontal
Par = Parietal
O = Operculum

Table 1. Length dimensions of 22 specimens of *Amia calva* L.: 21 from Wisconsin (MCZ 8970*), 1 from Michigan (UMMZ 197683)**
Measurements in mm

Specimen Code	Class Range Total Length	No.	TL	SL	ML	H	HL	Pf	P	C
1*	80.0	1	80.0	70.5	57.0	22.0	48.5	32.5	12.5	10.5
2*	95.0–105.0	2	100.0	85.0	70.0	25.0	60.0	39.5	16.0	15.0
3	207.0–212.0	6	210.0	175.0	145.0	50.5	124.5	80.9	35.0	35.0
4	227.9–232.0	4	230.0	193.0	161.0	54.6	138.4	88.5	35.5	36.0
5	241.0	1	241.0	199.0	165.9	56.8	142.2	93.5	38.0	42.0
6	291.0	1	291.0	237.0	197.0	64.0	173.0	115.0	52.5	54.0
7	310.0	1	310.0	248.0	207.0	68.5	179.5	112.0	46.0	62.0
8	339.0	1	339.0	274.0	230.0	73.0	202.0	125.0	51.0	64.0
9	385.0	1	385.0	313.0	259.0	82.0	231.0	142.0	52.0	72.0
10	433.0	1	433.0	349.0	293.0	91.0	258.0	170.0	71.0	84.0
11	475.0	1	475.0	399.0	335.0	103.0	296.0	181.0	82.0	76.0
12	507.0	1	507.0	423.0	359.5	109.0	317.0	192.0	93.0	81.0
13**	756.0	1	756.0	648.0	545.3	164.0	480.0	299.0	138.0	102.0

See Figure 2 for abbreviations.

this margin of error is graphically inconsequential in this study. Specimens of *A. calva* whose total length was between 207 mm and 507 mm were selected because this range of *A. calva* would provide the best information for comparison with the fossil species. Twenty-two specimens of *A. calva* were measured (Table 1). Eighteen of these are from the St. Croix River, Wisconsin. These 18 specimens of *A. calva* fall into ten categories arranged here by approximately 20–30-mm class range increments in total-length. Although these categories represent arbitrary rather than biological growth stages, they provide sufficient information on the morphologic size changes of *A. calva*. Three smaller specimens (MCZ 8970, also from Wisconsin) with a size range of 80–105 mm total length (TL) were included to determine whether they would follow the predicted allometric effect on the growth-series line, since, as Thomson and Hahn (1968: 205) note, it is a common feature for the early stages of juvenile animals to have heads proportionately larger than the bodies. Hay (1895) notes that an 80-mm *A. calva* is beyond the embryonic stage and is an early juvenile with most of its bones at least partially ossified. The 80-mm specimen has a proportionately larger head to standard-length ratio than the other members of the growth-series (Table 3). Although this ratio decreases slightly with increasing size, the head/standard-length ratio of 0.312 for the 80-mm specimen does not deviate far from the growth-series line (Figs. 3–4).

The largest specimen (UMMZ 197683) was used as a size limit for the other end of the growth-series continuum. It may be assumed that this fish had already reached the size or point of maturity at which fish normally begin to decrease their rate of growth. This specimen still retains the morphological proportions of the smaller specimens (Figs. 3–4) and, like them, falls remarkably close to the constant relative size-growth lines of the various proportions. Although from Michigan, this specimen does not appear to deviate from the growth-series line established by the Wisconsin specimens of *A. calva*. The Michigan specimen of *A. calva*, since it agrees with the growth-series continuum established by the Wisconsin specimens, is helpful in extending comparison to the larger fossil amiids: *"Paramiatus gurleyi"* (FMNH 2201), *Amia fragosa* (MCZ 5341), and *Amia uintaensis* (PU 13865), which are outside the size range of the Wisconsin sample.

General Proportions and Growth

Allometric growth, according to Gould (1966: 595), describes geometrically progressive change in shape or proportions with size, and is generally represented by a curvilinear line or, in certain cases, by a straight line in which the Y-intercept is significantly different from 0.

For the *Amia calva* growth series discussed here, the ordered pairs corresponding to the proportions in each series have been plotted on a graph, as well as the straight line corresponding to the equation $y = a + bx$ (of the best fit computed ac-

TABLE 2. LENGTH DIMENSIONS OF 6 ARTICULATED FOSSIL AMIIDS
Measurements in mm

	TL	SL	ML	H	HL	Pf	P	C
A. scutata PU 10172	$^{\mathrm{est}}404.0$	339.0	276.5	106.0	233.0	159.0	73.0	$^{\mathrm{est}}65.0$
A. scutata UMMP V-57431	—	388.0	313.8	121.0	267.0	183.0	83.0	—
A. kehreri BMNH P33480	249.0	191.0	160.8	59.2	131.8	89.0	38.5	58.0
"Paramiatus gurleyi" FMNH 2201	702.0	510.0	430.0	157.0	353.0	$^{\mathrm{est}}265.0$	78.0	192.0
A. fragosa MCZ 5341	575.0	455.0	383.0	142.0	313.0	210.0	75.0	115.0
A. uintaensis PU 13865	848.0	664.0	—	214.0	450.0	288.0	116.0	160.0

See Figure 2 for abbreviations.

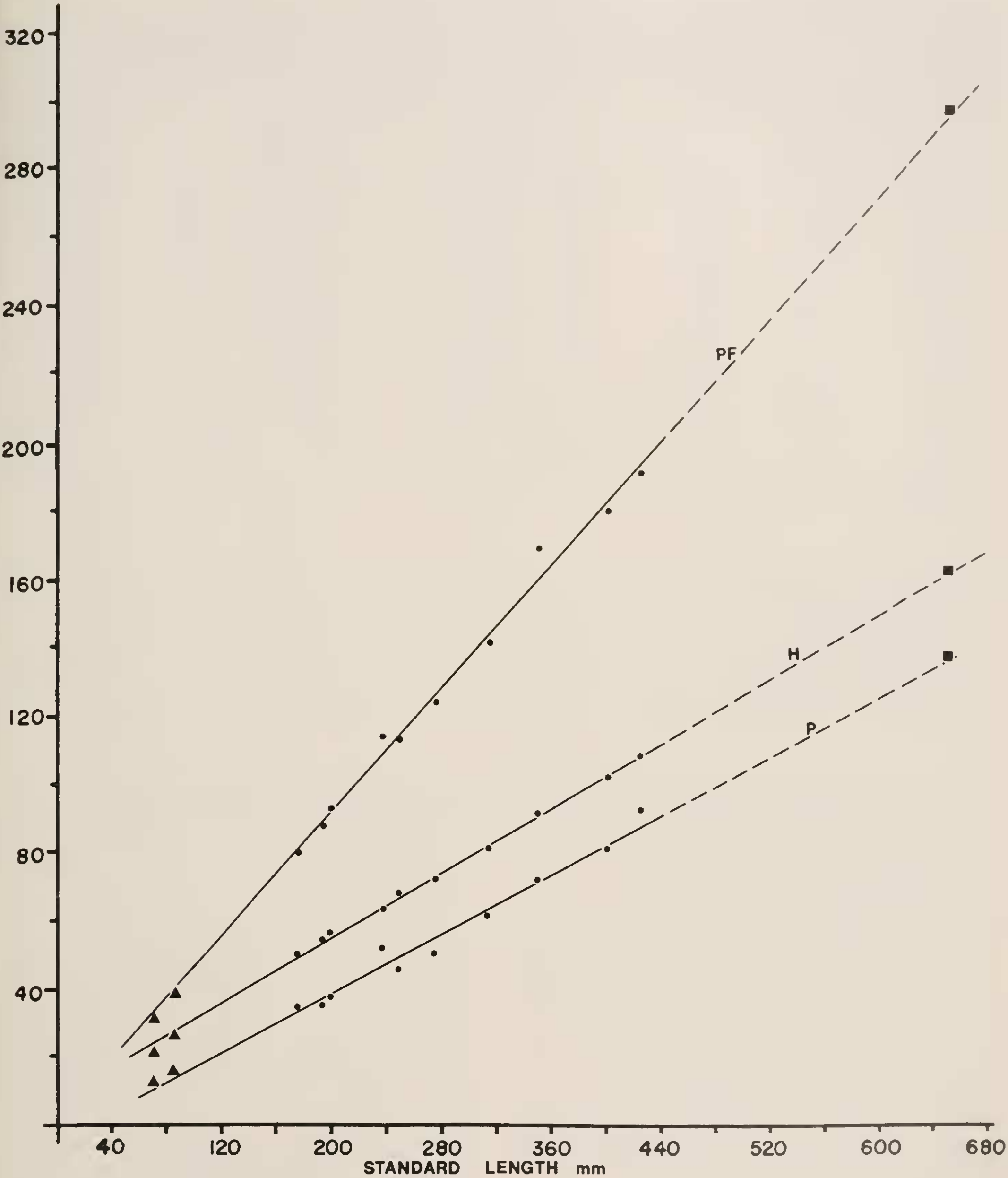


Fig. 3. Relative growth-lines of head-length (H), pelvic fin insertion (Pf), and anal fin insertion (P) plotted arithmetically against standard-length, for 18 specimens of Recent *Amia calva* (▲ = MCZ 8970 and ■ = UMMZ 197683 are included for comparison).

cording to the method of least squares); the results of these calculations appear in Figures 3–4. Practically all the ratios in Figure 3 fall onto straight lines, each of which nearly passes through the origin of the graph. The coefficient of correlation is almost equal to 1.0 in each case, an indication that the computed straight line provides

TABLE 3. COMPARISON OF LENGTH PROPORTIONS IN 22 SPECIMENS OF *Amia calva* WITH FOSSIL AMIIDS

Specimen Code	H/SL	Pf/SL	P/SL
1	0.312	0.461	0.177
2	0.294	0.464	0.188
3	0.289	0.462	0.200
4	0.283	0.459	0.184
5	0.285	0.470	0.191
6	0.270	0.485	0.222
7	0.276	0.452	0.185
8	0.266	0.456	0.186
9	0.262	0.455	0.198
10	0.261	0.487	0.203
11	0.258	0.454	0.206
12	0.258	0.454	0.220
13	0.259	0.461	0.213
	0.258–0.289* mean = (0.271)*	0.452–0.487* mean = (0.463)*	0.184–0.222* mean = (0.199)*
Oligocene			
A. scutata PU 10172	0.313	0.469	0.215
A. scutata UMMP V-57431	0.312	0.472	0.214
Eocene			
A. kehreri BMNH P33480	0.310	0.466	0.201
"Paramiatus gurleyi" FMNH 2201	0.308	^{est}0.520	0.153
A. fragosa MCZ 5341	0.312	0.462	0.165
A. uintaensis PU 13865	0.322	0.434	0.175

* Range and mean exclude Specimen Codes 1 & 2 (MCZ 8970) and 13 (UMMZ 197683).

a very good fit for the ratio series, and that the relative growth of these three dimensions is essentially isometric rather than allometric. The Wisconsin specimens (including the 80–105-mm specimens) and the larger Michigan specimen all fall close to the line calculated for each of the three ratios (Fig. 3). The proportions of head-length/standard-length, insertion of pelvic fins/standard-length, and insertion of anal fins/standard-length are shown in Table 3. The head/standard-length ratio shows a slight decrease with increasing size, but this ratio series nonetheless has a very high coefficient of correlation for the strength of the linear relationship (Fig. 4).

The lengths of the mandible, parietal, frontal, and operculum in Recent *A. calva* appear in Table 4, and the proportional ratios in Table 6. The relative growth rate of each of these proportions is constant with X and Y-intercepts of the straight line close to the origin. The coefficient of correlation for the variables in each of the proportions is 0.997, 0.975, and 0.997, respectively (Fig. 5). Combined, these two factors indicate constant and therefore isometric relative size-growth of the compared skull element.

Comparisons with Fossil Forms

Six articulated fossil specimens were available for measurement and calculation of head/standard-length and positions of insertion of pelvic and anal fins/standard-length (Tables 2–3). The measurements taken from the fossil forms are as exact as conditions allow, although it must be stressed that varying degrees of crushing and distortion have occurred in fossilization, and evaluation of the morphometrics should be qualified with this in mind.

Head/standard-length ratios (Fig. 4). The fossil forms all show a slightly greater head/standard-length ratio than does the Recent species (Table 3; Fig. 4). *A. uintaensis* (PU 13865) is the largest of

Table 4. Length dimensions of Mandible (M), Gular (G), Frontal (F), Parietal (Par), Infraorbital ^{5}(I^5), and Operculum (O) in 22 specimens of *A. calva*
Measurements in mm

Specimen Code	M	G	F	Par	I^5	Operculum Dors.-Vent. (OL)	Operculum Ant.-Post. (OD)
1*	13.5	8.0	10.0	5.0	5.0	8.1	7.5
2*	14.9	9.4	11.4	6.1	5.8	9.0	8.4
3	30.0	19.0	18.0	9.7	12.0	14.0	12.9
4	32.0	21.0	20.0	9.9	13.5	15.0	14.2
5	33.5	20.5	19.0	10.0	14.2	16.0	14.9
6	39.0	26.0	25.0	11.0	17.0	16.9	16.5
7	42.0	28.0	25.5	11.5	18.0	18.1	17.5
8	45.0	27.0	26.2	13.5	21.0	19.8	18.5
9	53.0	31.0	31.0	14.7	22.5	22.8	21.8
10	56.0	32.5	32.2	17.0	26.5	22.6	22.5
11	63.0	39.0	38.4	18.5	30.5	28.1	27.8
12	66.5	42.5	39.0	19.5	31.5	27.8	28.5
13**	102.7	—	60.7	30.0	—	—	—

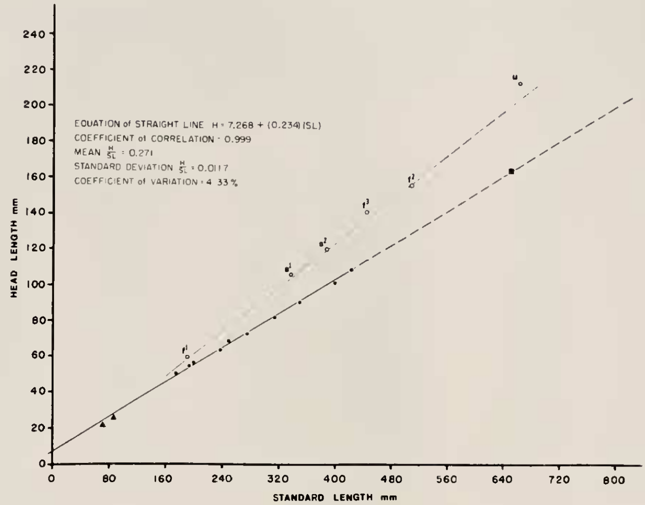
* MCZ 8970.
** UMMZ 197683.

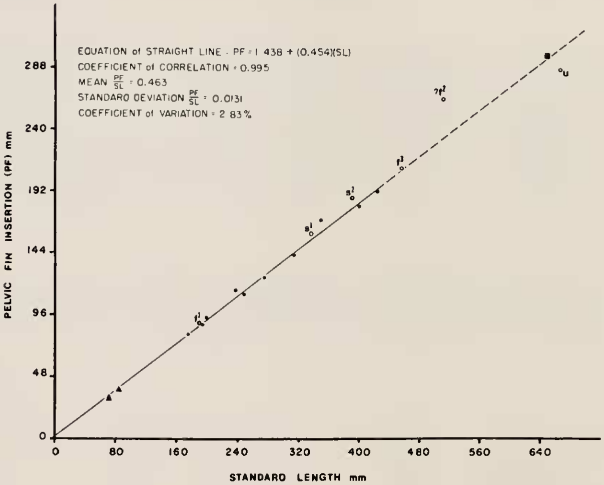
all the fossil specimens, but nonetheless has a greater head/standard-length ratio than any of the others. The head of this form is so much more elongated than the head in *A. fragosa* (MCZ 5341), *A. kehreri* (BMNH P33480), and "*Paramiatus gurleyi*" (FMNH 2201) that it offsets the fact that its vertebral column includes approximately 20 more vertebrae than do these three forms (Table 9). Thus, although *A. uintaensis*

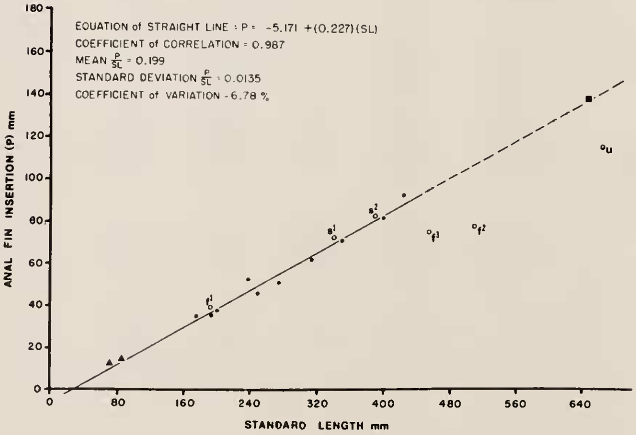
Table 5. Length dimensions of Head (H), Mandible (M), Gular (G), Frontal (F), Parietal (Par), Infraorbital ^{5}(I^5), and Operculum (O) in fossil amiids
Measurements in mm

	H	M	G	F	Par	I^5	Operculum Dors.-Vent. (OL)	Operculum Ant.-Post. (OD)
A. cf. *scutata* UCMP 38222	—	65.2	—	46.0	23.0	35.0	—	—
A. *scutata* PU 10172	106.0	62.5	31.2	35.0	16.0	—	29.0	28.0
A. *scutata* UMMP V-57431	121.0	74.2	—	44.3	20.0	—	29.1	27.9**
A. "*dictyocephala*" AMNH 2802	111.5	68.0	—	38.0	17.0	29.1	32.0	30.0
A. *kehreri* BMNH P33480	59.2	30.2	—	20.0	8.4	15.3	20.5	19.0
"*Paramiatus gurleyi*" FMNH 2201	157.0	80.0	—	58.0	23.6	25.0	40.0	37.0
A. *fragosa* MCZ 5341	142.0	72.0	68.7	56.0	22.8	—	39.0	36.2
A. *fragosa* MCZ 9264	80.0	40.0	—	26.0	10.5	18.5	—	—
A. *uintaensis* PU 13865	214.0	—	—	88.0	34.0	—	55.0	51.0
"*Protamia*" *mongoliensis* AMNH 6372	—	—	81.0	—	—	—	54.0	52.0
A. *uintaensis* PU 16236	315.0**	220.0	158.0	160.0	60.0	—	—	95.0
A. *fragosa* MCZ 9291	—	—	—	—	—	—	27.0	25.0
A. *fragosa* AMNH 9315	—	—	—	—	—	—	29.0**	27.0
A. *fragosa* UA 5450*	—	—	—	26.0	10.0	—	—	—
A. *fragosa* UA 5458*	—	—	—	30.0	12.0	—	—	—
A. *fragosa* UA 5480*	—	—	—	—	—	20.0	26.0	24.0

* Data from O'Brien (1969).
** Est.


EQUATION of STRAIGHT LINE H = 7.268 + (0.234) (SL)
COEFFICIENT of CORRELATION - 0.999
MEAN $\frac{H}{SL}$ = 0.271
STANDARD DEVIATION $\frac{H}{SL}$ = 0.0117
COEFFICIENT of VARIATION = 4 33 %
HEAD LENGTH mm
STANDARD LENGTH mm
0
20
40
60
80
100
120
140
160
180
200
220
240
0
80
160
240
320
400
480
560
640
720
800
f^1
s^1
s^2
f^3
f^2
u


EQUATION of STRAIGHT LINE - PF = 1 438 + (0.454)(SL)
COEFFICIENT of CORRELATION = 0.995
MEAN $\frac{PF}{SL}$ = 0.463
STANDARD DEVIATION $\frac{PF}{SL}$ = 0.0131
COEFFICIENT of VARIATION = 2 83 %
PELVIC FIN INSERTION (PF) mm
STANDARD LENGTH mm
0
48
96
144
192
240
288
0
80
160
240
320
400
480
560
640
f^1
s^1
s^2
f^3
?f^2
u


EQUATION of STRAIGHT LINE : P = -5.171 +(0.227)(SL)
COEFFICIENT of CORRELATION = 0.987
MEAN $\frac{P}{SL}$ = 0.199
STANDARD DEVIATION $\frac{P}{SL}$ = 0.0135
COEFFICIENT of VARIATION - 6.78 %
ANAL FIN INSERTION (P) mm
STANDARD LENGTH mm
0
20
40
60
80
100
120
140
160
180
0
80
160
240
320
400
480
560
640
f^1
s^1
s^2
f^3
f^2
u

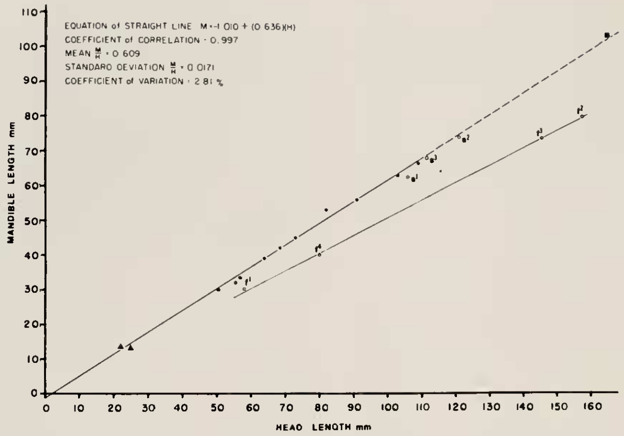
has significantly more vertebrae than these other forms, this feature is not reflected in a comparison of head/standard-length ratios (Table 3). This is also true, to a lesser extent, in both *A. scutata* specimens (PU 10172, UMMP V-57431) from the Oligocene Florissant Formation; these specimens fall into the head/standard-length range of the three fore-mentioned forms, but like *A. uintaensis*, possess vertebral columns having nearly the same number of centra as those in *A. calva*. Thus in themselves the head/standard-length ratios are of little help in comparing the fossil forms, but when coupled with the corresponding lengths of the vertebral column (based on number of centra) they are informative. *A. uintaensis* (PU 13865) and *A. scutata* (PU 10172, UMMP V-57431) have relatively elongated heads; *A. kehreri* (BMNH P33480), *A. fragosa* (MCZ 5341), and "*Paramiatus gurleyi*" (FMNH 2201) have relatively shorter heads, since the head/standard-length ratio is less than might otherwise be expected considering the smaller total-number of centra (only two-thirds the number of centra of *A. uintaensis, A. scutata*, and *A. calva*). A tentative growth-line (also calculated by the best-fit method) was included for *A. fragosa* on the basis of three specimens (Fig. 4). In comparison with the growth-line of the Recent species (0.271 mean), it reflects the larger head/standard-length ratio of *A. fragosa* (0.310 mean). The growth-line computed for *A. fragosa* is linear and falls near the origin, indicating that increase in head size/standard-length was isometric, as in *A. calva*.

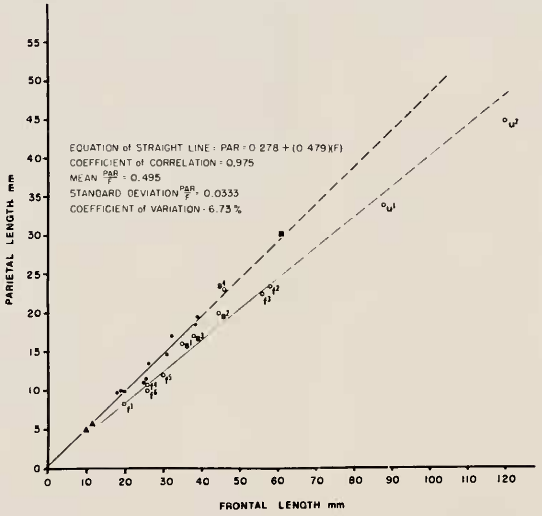
Fin relationships. In the smaller fossil forms, the ratio of the point of insertion of the pelvic fin/standard-length shows little deviation from the modern species (Table 3; Fig. 4) except for two Eocene specimens, "*Paramiatus gurleyi*" (FMNH 2201) and *A. uintaensis* (PU 13865), which fall outside of the range on either side of the size-growth line. The greater ratio for "*Paramiatus gurleyi*," however, is probably the result of distortion in its preservation. The length of the pelvic fin insertion/standard-length does not appear to be a satisfactory taxonomic index, distinguishing neither the fossil forms from one another nor the fossil forms from the Recent *A. calva*.

"*Paramiatus gurleyi*" (FMNH 2201), *A. uintaensis* (PU 13865), and *A. fragosa* (MCZ 5341) have a relatively shorter dimension between the anal fin and the end of the vertebral column than do *A. calva, A. scutata*, and *A. kehreri* (Fig. 31). Any attempt to interpret the fossil data for this ratio is complicated by the fact that considerable overlap with the Recent species occurs. Both long-bodied (*A. scutata*) and short-bodied (*A. kehreri*) forms fall within the range of *A. calva*, while other long-bodied (*A. uintaensis*) and short-bodied (*A. fragosa*, including "*Paramiatus gurleyi*") forms fall below the range of the Recent species (Table 3). Although the ratio of anal fin/standard-length may possibly be useful in distinguishing *A. fragosa* (including "*Paramiatus gurleyi*") from *A. calva, A. scutata*, and *A. kehreri*, it is not useful in distinguishing either of the two fossil forms from one another or from *A. calva*. The smaller dimension indicated by the low ratios (0.153, 0.165) of *A. fragosa* is doubtless a reflection of its shorter axial column. The relatively small (0.175) ratio for *A. uintaensis* is probably in part the result of its longer head, which increases its standard-length in relation to the other forms; at any rate, the difference between the *A. uintaensis* ratio and the range for Recent *A. calva* is not very significant.

Mandible/head ratios. A comparison of

Fig. 4. Relative growth-lines (broken-solid lines) of head-length, pelvic fin insertion, and anal fin insertion plotted arithmetically against standard-length for Recent *Amia calva* (▲ = MCZ 8970 and ■ = UMMZ 197683 are included for comparison) with compared fossil forms: f^1 = *A. fragosa (A. kehreri)* BMNH P33480; f^2 = *A. fragosa (Paramiatus gurleyi)* FMNH 2201; f^3 = *A. fragosa* MCZ 5341; s^1 = *A. scutata* PU 10172; s^2 = *A. scutata* UMMP V-57431; *u* = *A. uintaensis* PU 13865. The broken-dotted line is the "best fit" line for available specimens of *A. fragosa*.


EQUATION of STRAIGHT LINE M = -1 010 + (0 636)(H)
COEFFICIENT of CORRELATION - 0.997
MEAN M/H = 0 609
STANDARD DEVIATION M/H = 0 0171
COEFFICIENT of VARIATION : 2 81 %
MANDIBLE LENGTH mm
HEAD LENGTH mm
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
f1
f4
a1
a3
a2
f3
f2


EQUATION of STRAIGHT LINE : PAR = 0 278 + (0 479)(F)
COEFFICIENT of CORRELATION = 0.975
MEAN PAR/F = 0.495
STANDARD DEVIATION PAR/F = 0.0333
COEFFICIENT of VARIATION - 6.73 %
PARIETAL LENGTH mm
FRONTAL LENGTH mm
0
5
10
15
20
25
30
35
40
45
50
55
60
70
80
90
100
110
120
u1
u2
f1
f2
f3
f5
f6
a1
a2
a3
a4

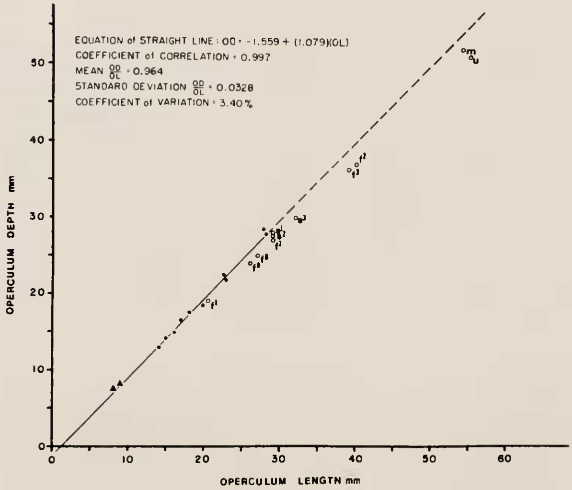

EQUATION of STRAIGHT LINE : OD = -1.559 + (1.079)(OL)
COEFFICIENT of CORRELATION = 0.997
MEAN OD/OL = 0.964
STANDARD DEVIATION OD/OL = 0.0328
COEFFICIENT of VARIATION = 3.40 %
OPERCULUM DEPTH mm
OPERCULUM LENGTH mm
0
10
20
30
40
50
60
f1
f2
f3
a3
m
u

Table 6. Cranial proportions in 22 specimens of *A. calva*

Specimen Code	M/H	Par/F	OD/OL
1	0.614	0.500	0.926
2	0.596	0.535	0.933
3	0.594	0.539	0.921
4	0.586	0.495	0.947
5	0.590	0.526	0.931
6	0.609	0.440	0.976
7	0.613	0.451	0.967
8	0.616	0.515	0.934
9	0.646	0.474	0.956
10	0.615	0.528	0.996
11	0.611	0.482	0.989
12	0.610	0.500	1.025
13	0.626	0.497	—
	0.586–0.646*	0.440–0.539*	0.921–1.025*
	mean = (0.609)*	mean = (0.495)*	mean = (0.964)*

* Range and mean exclude Specimen Codes 1 & 2 (MCZ 8970) and 13 (UMMZ 197683).

the mandible/head ratios of Recent *A. calva* with those of the fossil forms (Table 7; Fig. 5) indicates that the *A. scutata* and *A. "dictyocephala"* (AMNH 2802) ratios are very close to those of *A. calva*. The *A. fragosa* specimens (including "*Paramiatus gurleyi*" FMNH 2201 and *A. kehreri* BMNH P33480) have a mean mandible/head ratio of 0.507, which, when compared to the *A. calva* mean ratio of 0.609, indicates a relatively smaller mandible to head size (Table 7). Unfortunately, *A. uintaensis* (PU 13865) cannot be used in this comparison, since the mandibles are buried in matrix. A reconstruction of a disarticulated *A. uintaensis* (PU 16236) specimen from the Late Paleocene has been made, and its ratio is approximately 0.693. Thus mandible/head proportions may be valid for distinguishing specimens of *A. fragosa* and *A. uintaensis* from one another as well as from *A. calva* and *A. scutata*. This ratio, however, cannot be used as a valid criterion for distinguishing *A. scutata* from *A. calva*. The 0.693 mandible/head ratio of *A. uintaensis* indicates that this form has the largest mouth gape of the four valid species. A tentative growth-line for the mandible/head-length proportion of *A. fragosa*, established on four specimens, shows that its jaw is 16 percent smaller than that of *A. calva*, and in this respect confirms Romer and Fryxell's (1928) reconstruction of "*Paramiatus gurleyi*."

Parietal/frontal ratios. Only articulated frontals and parietals were measured for this study. The frontal-length was taken from the anteriormost extent of the dermal sculpture to the median point between the most anterior and posterior extents of the frontal-parietal suture; the parietals were also measured by their midline anteroposterior length. The parietal/frontal ratio of the fossil forms as compared with that of the Recent *A. calva* indicates that, in varying degree, the fossil species have relatively shorter parietals and longer frontals (Table 7; Fig. 5). The largest specimen of *A. uintaensis* (PU 16236) is mostly disarticulated, but fortunately the skull table is intact. It has the smallest parietal/frontal ratio of all the fossil species, 0.375. The Eocene *A. uintaensis* specimen (PU 13865) has a slightly larger ratio of 0.386, which is nearly equal to the Edmonton *A. fragosa* (UA 5450). All the other available *A. fragosa* specimens, including "*Paramiatus gurleyi*" (FMNH 2201), have slightly larger ratios and are quite consistent, ranging only

Fig. 5. Relative growth-lines (broken-solid lines) of mandible-length plotted arithmetically against head-length, parietal-length plotted arithmetically against frontal-length, and operculum-depth (anteroposteriorly) plotted arithmetically against operculum-length (dorsoventrally) for Recent *Amia calva* (▲ = MCZ 8970 and ■ = UMMZ 197683 are included for comparison when element measurements are available) with compared fossil forms: f^1 = *Amia fragosa (A. kehreri)* BMNH P33480; f^2 = *A. fragosa (Paramiatus gurleyi)* FMNH 2201; f^3 = *A. fragosa* MCZ 5341; f^4 = *A. fragosa* MCZ 9264; f^5 = *A. fragosa* UA 5458; f^6 = *A. fragosa* UA 5450; f^7 = *A. fragosa* AMNH 9315; f^8 = *A. fragosa* MCZ 9291; f^9 = *A. fragosa* UA 5480; s^1 = *A. scutata* PU 10172; s^2 = *A. scutata* UMMP V-57431; s^3 = *A. scutata (A. dictyocephala)* AMNH 2802; s^4 = *A.* cf. *scutata* UC 38222; u^1 = *A. uintaensis* PU 13865; u^2 = *A. uintaensis* PU 16236; m = *A. mongoliensis* AMNH 6372. The broken-dotted line is the "best fit" line for available specimens of *Amia fragosa*.

Table 7. Comparison of cranial proportions of recent and fossil amiids

	M/H	Par/F	OD/OL
Recent			
A. calva (18) (Wisc.)	0.586–0.646 mean = (0.609)	0.440–0.539 mean = (0.495)	0.921–1.025 mean = (0.964)
Miocene			
A. cf. *scutata* UCMP 38222	—	0.500	—
Oligocene			
A. scutata PU 10172	0.590	0.457	0.965
A. scutata UMMP V-57431	0.613	0.451	0.959
A. "dictyocephala" AMMH 2802	0.610	0.447	0.937
Eocene			
A. kehreri BMNH P33480	0.510	0.420	0.927
"Paramiatus gurleyi" FMNH 2201	0.509	0.407*	0.925
A. fragosa MCZ 5341	0.507	0.408	0.928
A. fragosa MCZ 9264	0.500	0.404	—
A. uintaensis PU 13865	—	0.386	0.927
"Pappichthys" mongoliensis AMNH 6372	—	—	0.963
Paleocene			
A. uintaensis PU 16236	0.693*	0.375	—
Cretaceous			
A. fragosa MCZ 9291	—	—	0.926
A. fragosa AMNH 9315	—	—	0.931*
A. fragosa UA 5450	—	0.385	—
A. fragosa UA 5458	—	0.400	—
A. fragosa UA 5480	—	—	0.923

* Est.

between 0.400–0.408. One of the specific character-states that Estes and Berberian (1969: 6) list for *A. fragosa* is a frontal-length of approximately 2.8 times the length of the parietals, which would give a ratio of 0.357. This figure is smaller than that of the known articulated forms, including the specimens from the Edmonton and Willwood formations. Although they may have placed too much emphasis on this specific character-state, Estes (1964), Janot (1967), and Estes and Berberian (1969) are justified in distinguishing *A. fragosa* from *A. calva* on this basis since the ratio of the fossil form is smaller than that of the Recent *A. calva*, whose parietal/frontal proportions have a mean ratio of 0.495, the frontals being approximately twice the length of the parietals. A tentative growth-line for parietal/frontal proportions, established on six specimens of *A. fragosa*, including *"Paramiatus gurleyi"* (FMNH 2201) and *A. kehreri* (BMNH P33480), illustrates this difference between the fossil form and the Recent species (Fig. 5). *A. kehreri* displays slightly larger parietals, with a ratio of 0.420, but considering the geographic and temporal differences from the other *A. fragosa* specimens, it is remarkably close in this feature to its North American relatives. The parietal/frontal proportions of the specimens of *A. "dictyocephala"* and *A. scutata* fall near the lower end of the 0.440–0.539 range of *A. calva*, and the Miocene specimen of *Amia* (UCMP 38222), with its ratio of 0.500, is very near the mean for *A. calva*. There is thus a definite trend from the Cretaceous to the Miocene (and Recent) toward an increase in parietal/frontal ratio. The *A. uintaensis* and *A. fragosa* specimens have parietal/frontal ratios smaller than those of *A. calva*, while the *A. "dictyocephala"* and *A. scutata* specimens are close to *A. calva* in this proportion. There is, however, enough intraspecific variation of parietal/frontal ratios in the fossil species to cause an interspecific overlap of the various forms, so that it is impossible to determine any definitive limits between the consecutive fossil species and *A. calva*.

Operculum-depth/operculum-length ratios. Although the fossil forms have a slightly narrower operculum-depth relative to their operculum-length, they all fall within the operculum ratio range of 0.921–1.025 for *A. calva* (Fig. 5). Table 6 indicates that with increasing size in *A. calva* there may be a trend from a narrower to a slightly broader operculum. Romer and Fryxell (1928: 521) describe the operculum of *"Paramiatus gurleyi"* as being greater dorsoventrally than anteroposteriorly. Although Cretaceous and Eocene specimens of *A. fragosa* have operculum ratios (0.923–0.963) lower than the mean (0.964) for *A. calva,* they still fall within the range (0.921–1.025) of the Recent form. Thus the variation of operculum shape within *A. calva* contradicts Hussakof's (1932) supposition that the operculum in *"Pappichthys" mongoliensis* (with a ratio of 0.963) is proportionately narrower than that of *A. calva,* as well as Estes and Berberian's (1969) diagnosis that *A. fragosa* has a relatively shorter operculum-length as compared with height than *A. calva.* Janot (1967) was also cautious in assigning taxonomic importance to the operculum proportions because of the great variability within the Recent species. The operculum width/length ratios in the fossil specimens show little taxonomic significance, although, as Estes and Berberian (1969: 7) note, there does appear to have been a slight temporal trend toward a broader operculum.

Discussion

The six relative growth proportions (Figs. 4–5) that were plotted for the *A. calva* growth-series remained constant and therefore isometric. This may be explained by the fact that these ratios are derived from external rather than internal dimensions, and, as Gould (1966) points out, it is usually the internal elements that must increase at an allometric rate in order to maintain the external surface area, whose dimensions may be increasing at an isometric rate (see meristic study). It may be assumed that the relative growth for these six proportions also maintained an isometric rate in the fossil forms, since their ratios invariably fall near the growth-lines for the Wisconsin *A. calva* sample (Figs. 4–5). However, this assumption would have to be confirmed with an actual growth-series of the fossil forms.

The comparison of Recent with fossil forms has also made it possible to determine the taxonomic value of the skull/body and skull proportions. The morphometric comparison of the fossil forms with Recent *A. calva* suggests the following taxonomic and phylogenetic trends:

1. All the fossil forms have slightly longer heads relative to their standard-length than does the Recent species (Fig. 31). Unless the differences in vertebral meristics are also considered, however, the morphometric data for this feature are not useful in comparing the various fossil forms. *A. uintaensis* and, to a lesser extent, *A. scutata* have relatively longer heads with a vertebral column of approximately 85 centra. *A. fragosa,* on the other hand, is a short-bodied form (approximately 65 centra) with a short head. *A. calva* has a relatively long vertebral column (81–90 centra) with a shorter head than the other long-bodied forms (*A. uintaensis* and *A. scutata*).
2. Pelvic fin insertion has no taxonomic significance.
3. Anal fin insertion may have minor taxonomic significance for the North American specimens of *A. fragosa* which are relatively shorter in this dimension than in the other species. There is too much morphological overlap between

the species, however, to make this a useful criterion.

4. *A. uintaensis* has a relatively longer mandible/head ratio (0.693) than any of the other species of *Amia,* while *A. fragosa* has a smaller ratio (0.507 mean). The mandible/head ratio of *A. scutata* (0.604 mean) is close to that of *A. calva* (0.609 mean).
5. There is a trend from the Late Cretaceous to Late Miocene in the lengthening of the parietals in relation to the frontals. Although it is possible to discern groups that fall into categories of smaller and larger ratios (Table 7), interspecific morphological overlap makes it difficult to separate any one of the fossil species from the others on this criterion.
6. All the fossil forms have operculum depth/width proportions that fall into the lower limits of the *A. calva* range (0.921–1.025). These ratios show a slight temporal trend towards increasing width, but, while this is perceptible, it is insufficient to indicate taxonomic significance.

These trends suggest possible phylogenetic relationships between the various amiid species. The morphometric similarities indicate that little evidence exists for maintaining *A. scutata* and *A. "dictyocephala"* as separate species. The Oligocene *A. scutata* is distinguishable quantitatively from *A. calva* only on the basis of a larger head/standard-length ratio, and in this feature it is intermediate between *A. calva* and *A. uintaensis.* The morphometric evidence indicates similarities between *A. fragosa* (Cretaceous-Eocene), *"Paramiatus gurleyi"* (Eocene), and *A. kehreri* (Eocene). Head/standard-length ratio is approximately the same among these three forms; insertion of anal and pelvic fins/standard-length ratios shows only minor differences. Mandible/head size and parietal/frontal ratios are almost identical. Of all the species, *A. uintaensis* is the most morphometrically distinct. It has a relatively greater mandible/head ratio and a smaller parietal/frontal ratio than *A. fragosa* (Table 7). Even though it possesses approximately the same total number of centra as *A. calva* and *A. scutata* (Table 9), it still has a greater head/standard-length ratio than the two latter species. Temporally, there are minor trends in *Amia* towards lengthening of the parietals in relation to the frontals, and increasing operculum width to depth.

MERISTICS

Meristic elements have been used in species diagnoses of various fossil amiids by Cope (1875), Osborn *et al.* (1878), Romer and Fryxell (1928), and Estes (1964). A meristic study of both Recent and fossil species of *Amia* was undertaken to determine the relative value of such diagnoses in the taxonomy of the amiids. A comparison of the number of supravertebral scale rows, the number of branchiostegal rays, and the number of pectoral, pelvic, anal, dorsal, and caudal fin rays comprises the first part of the study, while comparative vertebral meristics comprise the second part.

Supravertebral Scale Rows

Cope (1875) differentiated *A. scutata* from *A. calva* and *A. "dictyocephala"* on the basis of *A. scutata's* (USNM 5374) having seven and a half longitudinal rows of large scales above the vertebral column. Cope (1875) described *A. "dictyocephala"* (USNM 3992) as bearing ten to twelve rows of scales above the vertebral column. A count of the scale rows between dorsal fin distal pterygiophores and the vertebral column in 20 Recent *A. calva* (Table 8) gave a range of seven to nine supravertebral scale rows. Although the number of scale rows will vary with the region of the trunk anatomy from which the count might be taken, Cope did not designate the point at which he made his scale row count. Also, his specimen was so poorly preserved that his count may have been affected by distortion of the scales. The only way that a valid comparison of all the forms could be made was

TABLE 8. COMPARISON OF MERISTIC ELEMENTS IN RECENT AND FOSSIL NORTH AMERICAN AMIIDS

	Supra-vertebral Scale Rows	Branchi-ostegal Rays	Pectoral-Fin Lepido-trichia	Pelvic-Fin Lepido-trichia	Anal-Fin Lepido-trichia	Dorsal-Fin Lepido-trichia	Caudal-Fin Lepido-trichia
Amia calva (20)	7–9	10–13	16–19	7–8	8–11	45–49	23–27
Recent	7.5 av.	11.4 av.	16.8 av.	7.2 av.	10.5 av.	48.0 av.	25.7 av.
A. scutata							
YPM 6243*							
USNM 4087*							
PU 10172*	7	11	—	7	9	47**	—
A. scutata							
USNM 5374	7.5	—	—	—	9	—	—
A. scutata							
YPM 6241	8	—	—	—	9	—	23
A. scutata							
UMMP V-57431	7	11	17	7	9	46**	—
A. "dictyocephala"							
USNM 3992	7.8	—	—	7	9	48**	—
A. "dictyocephala"							
AMNH 2802	—	11	—	—	—	—	—
A. "dictyocephala"							
AMNH 2670	9**	—	—	—	—	47**	—
A. uintaensis							
PU 13865	7	—	16	9	9**	—	23
A. uintaensis							
AMNH 785	9**	—	—	7	10	—	24
A. fragosa							
MCZ 5341	8	12	18	7	8	45	19–20
"Paramiatus gurleyi"							
FMNH 2201	7–8	12	17	8	8	44–45**	19
A. fragosa							
UA 5506	—	10	—	—	—	—	—
A. fragosa							
UA 5425	—	—	—	—	—	—	19

* All one specimen.
** Est.

to take the supravertebral scale row count of both the USNM 3992 specimen and the other fossil and Recent amiid specimens at the same point. In this case, I took all counts on a vertical line at the level of the posterior pterygiophore of the anal fin. I counted the number of scale rows in specimens of *A. fragosa*, *A. uintaensis*, and "*Paramiatus gurleyi*" in addition to those of Cope's types of *A. scutata* (USNM 5374) and *A. "dictyocephala"* (USNM 3992), as well as referred specimens of *A. scutata;* I then compared them with the supravertebral scale row range in *A. calva*. The supravertebral scale rows of fossil *Amia* (Table 8) appear to fall within the supravertebral scale row range of Recent *A. calva*. Although Cope had described *A. "dictyocephala"* (on the basis of USNM 3992) as having 10–12 scale rows, I believe his count is too high. The supravertebral scale rows in this and other fossil forms are difficult to observe for several reasons. Amiid scales are aligned diagonally to the vertebral column rather than in parallel, making it often difficult, particularly in fossil material, to determine to which diagonal column the overlapping scale rows belong. Also, the scales on the USNM 3992 specimen are broken into many parts, and Cope may therefore have been counting partial scales as whole ones. I believe that I obtained a more reasonable estimate of the supravertebral scale row count in this specimen in the following manner: I measured the average of the anteroventral width of complete scales from the abdominal region (in which the scales are the same size as in other places in the mid-body region) and then divided that amount into the distance between the midpoint of the vertebral column and the dorsal fin distal pterygiophore. In this case, the quotient was 7.8, which is comparable with the counts of approximately 7–9 in the other Oligocene specimens and in *A. calva* (Table 8). No taxonomic significance can thus be applied to the number of scale rows above the vertebral column since counts in Recent and fossil *Amia* fall within a relatively narrow range.

Branchiostegal Rays

The number of branchiostegal rays was included in the species diagnosis for *A. "dictyocephala"* (AMNH 2802), in which Cope (1875) counted 12 rays. Osborn *et al.* (1878) observed 13 branchiostegal rays in *A. scutata* (PU 10172) and Romer and Fryxell (1928) figured 12 such rays for *"Paramiatus gurleyi"* (FMNH 2201). O'Brien (1969) counted 10 rays in *A. fragosa* (UA 5506) from the Edmonton Formation. On the basis of disarticulated material from the Late Cretaceous Lance Formation, Estes (1964) estimated that *A. fragosa* would bear 14 branchiostegal rays, like the Late Jurassic *Sinamia zdanskyi* described from China by Stensiö (1935; see Liu *et al.*, 1963 for range and distribution). In the Recent *A. calva* sample (Table 8), the number of branchiostegal rays ranges from 10 to 13; the range among the few known examples of fossil forms is from 10 to 13, an indication that the number of branchiostegal rays has remained constant.

Fin Rays

Because of confusing duplication of terminology used for fin description in the literature, I will use that of Lagler *et al.* (1962) for the appendicular skeleton unless I indicate otherwise.

All fin ray counts on Recent *A. calva* were obtained from X-rays of 20 specimens from Wisconsin and Michigan. The counts taken from fossil forms are as accurate as conditions allow, although a number of the specimens are incomplete or show only traces of the actual fin. The results of this study must therefore be considered with this in mind. I obtained these counts from as close as possible to the internal fin supports rather than to the segmented and bifurcated distal lepidotrichia. There is a one-to-one correspondence between the number of lepidotrichia and the number of pterygiophores in the anal and dorsal fins; however, this is not the case in the pectoral, pelvic, and caudal fins, which have more lepidotrichia than fin supports (Fig. 31).

Pectoral fin. The number of pectoral fin lepidotrichia has not been previously noted in any of the original species descriptions of fossil *Amia.* There are four specimens in which it is possible to make a pectoral fin ray count (Table 8). *A. scutata* (1), *A. uintaensis* (1), and *A. fragosa* (2) specimens bear 16 to 18 pectoral lepidotrichia, a number which is approximately the average for 20 specimens of Recent *A. calva* which displayed from 16 to 19 pectoral fin rays (Table 8). O'Brien's (1969) analysis of *A. fragosa* (Edmonton Formation) does not include any quantitative comparison of its pectoral fins with those of *A. calva.* He does, however, observe that the pectoral fins are qualitatively similar in the two species. The pectoral fins of *A. fragosa, A. scutata,* and *A. uintaensis* thus do not vary meristically from those of *A. calva.* Lehman (1951: 8), in his description of *Pseudamia heintzi* from the Eocene of Spitzbergen, notes that the pectoral fin has 13 complete nonbifurcating lepidotrichia in the visible portion of the fossil. This count is different from that of both Recent and fossil North American amiids, but as Lehman's plate 3 indicates, this difference may be caused by matrix that overlies the ventral portion of the pectoral fin, possibly covering additional lepidotrichia.

Pelvic fin. The number of lepidotrichia of the pelvic fin was part of Cope's (1875) species diagnosis for *A. "dictyocephala"* (USNM 3992) and that of Osborn *et al.*

(1878) for *A. scutata* (PU 10172). I counted the lepidotrichia of these specimens as well as those of one additional Oligocene specimen and compared them with my sample of *A. calva*, which showed between seven and eight pelvic lepidotrichia (Table 8). Although Osborn *et al.* (1878) counted ten pelvic lepidotrichia, my recount of their *A. scutata* specimen (PU 10172) showed only seven (Plate 4). The bifurcation of the fin rays might have been inadvertently included in their original count. The holotype of *A. "dictyocephala"* (USNM 3992) (Fig. 27) showed seven rather than the six lepidotrichia that Cope (1875) had diagnosed. A specimen of *A. scutata* (UMMP V-57431) (Fig. 27A) also has seven lepidotrichia; both of these are within the range of Recent *A. calva*. Of the remaining fossil forms, *A. fragosa* and *"Paramiatus gurleyi"* have eight, and *A. uintaensis* nine, *A. uintaensis* being the only fossil form not to fall within the range of Recent *A. calva*. This difference is insufficient to demonstrate any taxonomic value, however, at least until more *A. uintaensis* specimens are known.

Anal fin. Anal fin lepidotrichia have been included in the diagnoses of *A. "dictyocephala"* and *A. scutata* (Cope, 1875), and also in the description of *A. scutata* (Osborn *et al.*, 1878). Each of the original counts of nine anal rays for each specimen concurs with my recount and also falls within the range of eight to eleven for Recent *A. calva* (Table 8). *A. fragosa*, *"Paramiatus gurleyi,"* and *A. uintaensis* also fall within the range of *A. calva*.

Dorsal fin. Although the number of lepidotrichia in the dorsal fin has been mentioned by several authors in their diagnoses of fossil amiids, it is one of the more difficult meristic counts to obtain, since a complete dorsal region of the fossil is required. Cope's type of *A. "dictyocephala"* (USNM 3992) lacks a complete dorsal fin, so he counted only the 32 dorsal lepidotrichia between the beginning of the dorsal fin and the posterior lepidotrichia of the anal fin (Cope, 1875). Osborn *et al.* (1878) reported 53 dorsal lepidotrichia for *A. scutata* (PU 10172), but this must have been an estimate, since the posterior portion of the dorsal fin as well as the entire caudal fin is missing (Plate 4C). As the two *A. scutata* specimens with complete dorsal fins (AMNH 2670, UMMP V-57431) have, respectively, 47 and 46 dorsal lepidotrichia (Table 8), it seems that the count of Osborn *et al.* (1878) was high and that the PU 10172 specimen would probably have corresponded with the other Oligocene specimens.

Romer and Fryxell's (1928) diagnosis for *"Paramiatus gurleyi"* includes a dorsal fin ray count of 45, which they note as being slightly fewer than the count for *A. calva*. O'Brien's (1969) discussion of Edmonton Formation *A. fragosa* does not include any counts of dorsal lepidotrichia, although he does note that the relative length of the entire dorsal fin in *A. fragosa* is similar to that of *A. calva*. In the *A. calva* specimens I studied, the dorsal fin rays ranged between 45 and 49, the average approximately 48. Romer and Fryxell's diagnosis of *"Paramiatus gurleyi"* as having slightly fewer dorsal lepidotrichia than *A. calva* is correct, but this and all the related fossil forms fall within the lower range of *A. calva* (Table 8). The number of dorsal fin rays appears to have little taxonomic value.

It is interesting that the complete *Amia fragosa* (MCZ 5341), *"Paramiatus gurleyi"* (FMNH 2201), and *A. kehreri* (BMNH P33480) specimens have dorsal fins of nearly the same length and contain the same number of lepidotrichia as *A. calva*, despite the fact that, on the basis of the number of vertebrae, these species have a much shorter body (Table 9). This contributes to a proportional difference in the body forms of these species, since the dorsal fin in *A. fragosa* (including *"Paramiatus gurleyi"*) terminates much closer to the caudal fin than in *A. calva* (Plate 1; Fig. 31). However, as Shufeldt (1885) and Hay (1895) implied, it is very doubtful that the dorsal fin was fused into a continuous structure with the caudal fin in some ancestral amiid. The Late Mesozoic European forms of *Urocles* and *Amiopsis* have a much abbreviated dorsal fin that terminates more anteriorly than does that of the species of *Amia.* For *Amiopsis dolloi,* an Early Cretaceous (Wealden) amiid from Bernissart, Belgium, Traquair (1911) figured 17 dorsal fin supports, while Lange (1968) establishes a specific range of 17–25 for the Eu-European Upper Jurassic *Urocles.* The basis of Shufeldt's (1885: 85–86) model for a primitive amiid with a continuous dorsal-caudal fin was the presence in Recent *Amia calva* specimens of what Shufeldt called a "series of delicate little bones that continue the interspinous bones of the dorsal fin as far as the caudal fin." These five bones he considered to be the continuation of the dorsal interneural spines; Hay (1895), in his discussion of *Amia calva,* refers to them as "epural interspinous bones." These small bones can also be seen in several of the fossil amiids I have studied, especially *A. scutata* (YPM 6241), *A. fragosa* (UA 5425), and *A. uintaensis* (AMNH 785) (Fig. 8). From these fossil forms, however, it is difficult to determine whether the origin of these bones is from the dorsal or caudal neural spines. An examination of the caudal fin of *Urocles lepidotus* (Fig. 6; also Nybelin, 1963: 506, fig. 17), which is known to have an abbreviated, more anteriorly located dorsal fin, shows that these epural bones are associated with the caudal fin, which supports the upper caudal lepidotrichia in much the same manner as the hypurals in the ventral tail region. A further indication that these epural interspinous bones are not vestigial dorsal spine supports is found in Traquair's (1911) plate 7 of *Amiopsis dolloi* and his plate 8 of *Amiopsis lata* (both species from the Cretaceous [Wealden] of Belgium); these plates show the bones to be clearly associated with the caudal lepidotrichia (Fig. 7).

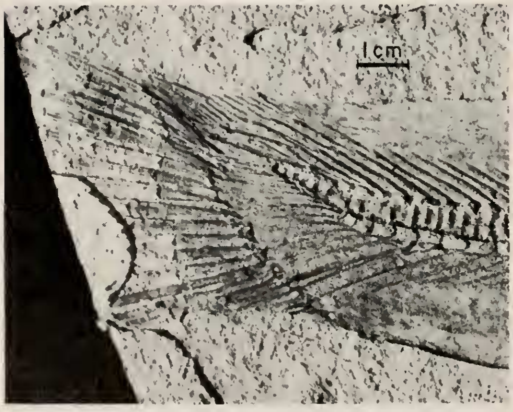


Fig. 6. *Urocles lepidotus* MCZ 8300, caudal fin.

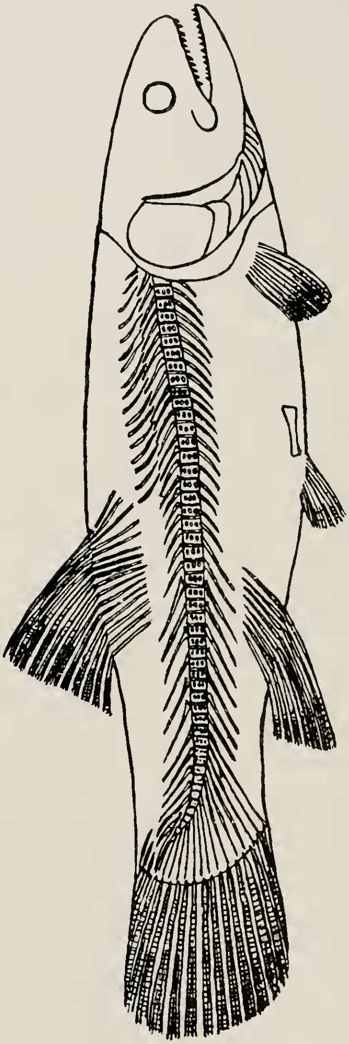


Fig. 7. Restoration of *Amiopsis dolloi,* scales omitted Early Cretaceous (Wealden), Bernissart, Belgium (after Traquair, 1911).

There are no intermediate interspinous bones between these bones in the caudal region and those of the much more anteriorly situated dorsal spine. The fin of a 648-mm SL Recent *Amia calva* (Fig. 10) does, however, confirm that Shufeldt (1885) was correct in stating that the epurals are continuations of the interneural spines. Figure 10 shows three free interspinous epurals, with a fourth that is either being fused onto a neural spine or is actually a single greatly elongated neural spine. As only two of these epurals are attached to lepidotrichia, there is not a one-to-one correspondence between the two elements, as in the hypurals in the main caudal region.

Caudal fin. With the exception of Romer and Fryxell's (1928) diagnosis of "*Paramiatus gurleyi*," none of the original descriptions of fossil *Amia* include counts of the caudal fin rays. Although Romer and Fryxell observed 20 caudal lepidotrichia, a recount shows only 19 (Fig. 8E). Other fossil forms that also show 19 caudal fin rays are *A. fragosa* (UA 5425) from the Edmonton Formation, *A. fragosa* (MCZ 5341) from the Green River Formation, and *A. kehreri* from Messel (Andreae, 1895, plate 1, fig. 23). Another specimen of *A. kehreri* from Messel (BMNH P33480) has 18 lepidotrichia (Plate 2). Traquair's (1911) plate 7 of three specimens of *Amiopsis dolloi* shows between 15 and 17 caudal lepidotrichia, while *Urocles* spp. have a range between 12–18 caudal lepidotrichia (Lange, 1968). The only Oligocene specimen with a complete caudal fin (YPM 6241) has 23 caudal lepidotrichia; the Eocene specimens of *Amia uintaensis* show 23 to 24. Although my sample of *Amia calva* displays caudal fins with a range of 23 to 27 lepidotrichia, the number of these caudal fin rays is skewed toward the higher limit of the range (Fig. 9). There is thus a considerable difference between the number of lepidotrichia in *Amia fragosa* and the majority of the *A. calva* specimens. *A. scutata* is, however, within the range of the Recent species, but occupies the lower limits of the range.

Thus, of all the meristic elements so far considered, it appears that the greatest disparity between the fossil forms and the Recent *A. calva* is in the number of caudal fin rays. The number of caudal fin rays therefore appears to have taxonomic importance and may have some functional as well as morphological correspondence to the two different amiid body types.

As discussed in the preceding section on dorsal fins, there are two attachment bases for the caudal lepidotrichia: epural interspinous bones and the hypurals. The epurals are usually attached to only two or three of the caudal fin rays, while the remainder of the lepidotrichia are supported by the hypurals. Nybelin (*in* 1963: 488) defines hypurals as "those haemal elements located to the rear of the emergence of the caudal artery from the haemal canal" (trans. Lund, 1967: 210) (Fig. 10B). Lund (1967: 210) agrees instead with Whitehouse (1910: 592), who defines hypurals as "any hypaxial elements that support caudal fin rays" (Fig. 10A). Lund states that the sole function of a hypural is to support a caudal fin ray and therefore the first hypural would be "the first haemal spine in rearward progression to support a caudal fin ray and the first ural centrum is the centrum supporting the first hypural element." Lund's definition is more practical for paleontological use. Since there is an intermediate joint (Figs. 8, 10), the majority of the hypurals are not attached directly to the urals. However, as Shufeldt (1885) and Hay (1895) observed, the posteriormost seven to nine hypurals are ankylosed to the corresponding vertebrae (Fig. 10C). This same co-ossified condition of the last hypurals is also evident in the fossil forms, so that the number of these fused hypurals has remained constant throughout the evolutionary history of *Amia*. Also, as Figure 10 shows, the seven or eight anteriormost hypurals of Recent *A. calva* have a one-to-two correspondence with the ventral lepidotrichia. In most of the available fossil amiid specimens, the ventral caudal portion is poorly preserved, so that it is difficult to

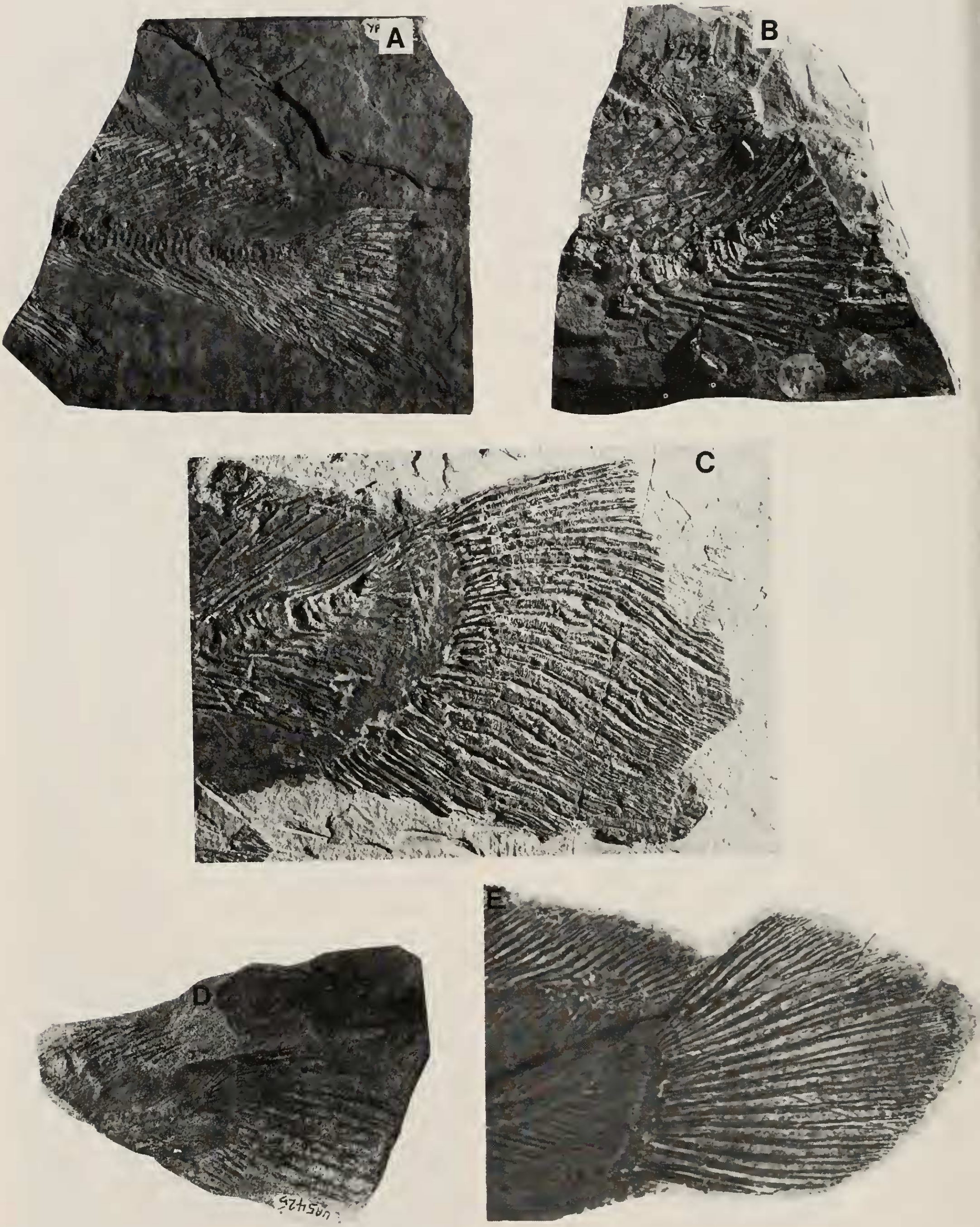


Fig. 8. Caudal regions: A, *Amia scutata* YPM 6241; B, *A. scutata* AMNH 2671; C, *A. uintaensis* AMNH 785; D, *A. fragosa* UA 5425; and E, *A. fragosa* FMNH 2201.

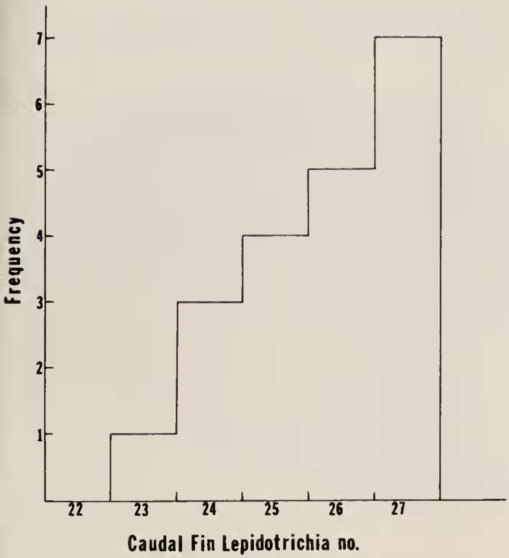


Fig. 9. Number of caudal lepidotrichia in 20 specimens of Recent *Amia calva*.

arrive at an accurate count of the total number of hypurals or to verify whether this one-to-two relationship exists in all the amiid fossil forms. The only available fossil form in which this one-to-two hypural-lepidotrichia correspondence in the ventral caudal region can clearly be seen is in *A. scutata* (YPM 6241; Fig. 8).

Vertebral Elements

Two regions of the vertebral column, the trunk and the caudal regions, are defined by their relationships to the ribs, neural arches, and haemal arches. The trunk region consists of monospondylous vertebrae that possess paired basapophyses having gradually changing angles, dorsal neural facets, and ventral aortal facets. The number of trunk vertebrae in my sample of *Amia calva* varies from 36 to 38. The caudal region consists of three types of vertebrae, listed from anterior to posterior: regular monospondylous centra bearing neural and haemal arches, diplospondylous centra bearing neither neural nor haemal arches (neural and haemal facets still present), and ural centra. Since the neural and haemal facets are still present in the diplospondylous centra, there is no way to differentiate the latter from the monospondylous type in a disarticulated state. In my sample of *A. calva,* the number of regular caudal monospondylous centra (24–26) fluctuates by two centra, that of the diplospondylous caudal centra (14–17) by three (Table 9).

The posterior caudal region of *A. calva* consists of two types of urals: centra with hypurals attached by a layer of cartilage (free urals), and centra that are fused directly onto the hypurals, often lacking the neural arches (fused urals). When disarticulated, the fused urals can often be distinguished from the free urals, since part of the hypural usually remains fused to the ural, extending the posterior articular surface downward. The nonfused (free) urals cannot be distinguished in a disarticulated state from the monospondylous or diplospondylous caudal centra. The number of urals with fused hypurals is readily counted, since they are distinguishable from the remainder of the vertebrae. In order to identify a free ural, it is necessary to observe the relationship between the ural and its corresponding hypural and lepidotrichia. It is often difficult to make this distinction between free and fused urals, since the caudal region is seldom complete in articulated fossil forms. In *A. calva* the number of urals with ankylosed hypurals ranges between seven and nine. There are approximately seven principal urals fused to hypurals, followed by one or two small additional urals that do not articulate with the preceding vertebrae but lie dorsal to the upturned portion of the vertebral column. Because it is difficult to discern these urals in smaller specimens of *A. calva,* the count may be slightly biased, and a comparison of the fossil forms with the range established for *A. calva* must be made with this consideration in mind.

I counted the number of centra between the anterior dorsal fin pterygiophore and the posterior anal fin pterygiophore, since Cope (1875) used the number of central elements between these points as a specific character for *A. "dictyocephala"* (USNM

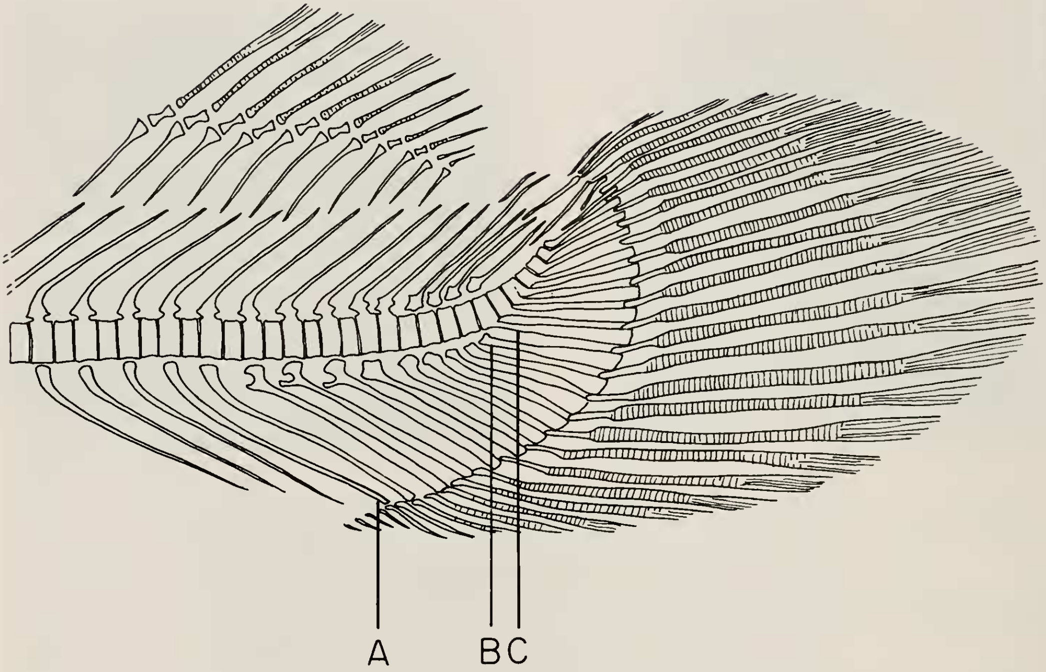


Fig. 10. *Amia calva* (648 mm SL) caudal: A, Whitehouse (1910) and Lund's (1967) definition of first ural; B, Nybelin's (1963) definition of first ural; C, first fused ural.

3992). The range for the number of centra in this region of Recent *A. calva* is 33 to 37.

There is considerable variation in total number of centra (*i.e.*, segments) in Recent *A. calva* (81–90), which may pose a problem in comparing specific vertebrae. Thus in two *A. calva,* for example, the eightieth vertebral segment of one individual might not correspond to the same position in the vertebral column or even type of centrum as the eightieth segment of the second individual. This should be considered in any comparisons of several *A. calva* individuals, as well as in comparisons of the fossil forms, which share this variation in vertebral segments (Table 9). Also, fusion of vertebral elements may occur in Recent *A. calva.* In some specimens, as many as five centra were found fused together at points throughout the vertebral column; this condition was present to a lesser degree or absent in other specimens (Tables 10–12). These fused centra also occur in the fossil forms, as in *A. uintaensis* (YPM 6244). The actual number of such fused centra can often be established only by counting external features such as basapophyses, neural facets, aortal facets, or haemal facets.

Romer and Fryxell's (1928) study of "*Paramiatus gurleyi*" is the only published description of a complete articulated fossil amiid. They distinguished this form from the Recent species by the supposed presence of a deeper body, and also noted that the number of centra was considerably less than in *A. calva.* The vertebral column is completely preserved, so that it is possible to obtain an accurate count of the vertebrae (Plate 1B). "*Paramiatus gurleyi*" has 67 vertebral segments in contrast to the mean of 86 in *A. calva* (Table 9). Osborn *et al.* (1878) described *A. scutata* (PU 10172) on the basis of a specimen lacking a caudal fin (Plate 4). Since the specimen is otherwise complete, they were able to estimate that their specimen had 82 vertebral segments.

Cope (1875) described *A. "dictyoce-*

Table 9. Comparison of vertebral characters in recent and fossil amiids

	Total Number of Centra**	Number of Trunk Centra	Number of Monospondylous Caudal Centra	Number of Diplospondylous Caudal Centra	Number of Ural Centra with Fused Hypurals	Number of Centra between Anterior Dorsal-Fin Pterygiophore and Posterior Anal-Fin Pterygiophore*
Recent						
Amia calva (20)						
Wis. & Mich.	81–90 mean = 85.8	36–38 mean = 37.3	24–26 mean = 25.2	14–17 mean = 16.2	7–9 mean = 8.3	33–37 mean = 35.5
Oligocene						
A. scutata						
PU 10172	83***	36	25	15	7***	35
A. scutata						
UMMP V-57431	81***	36	24***	15***	7***	37
A. "dictyocephala"						
USNM 3992*	—	—	—	—	—	35
Eocene						
"Paramiatus gurleyi"						
FMNH 2201*	67	26	19	16	6	26
Amia uintaensis						
PU 13865	85	31	26	21	7	36
Amia uintaensis						
AMNH 785	—	—	25	20	7	—
A. fragosa						
MCZ 5341	65	25	18	15	7	25
A. kehreri						
BMNH P33480	62***	24	16	16	6***	24

* = types.
** = including diplospondylous units (as one).
*** Est.

phala" from a specimen (USNM 3992) in which only the mid-body region was preserved. He felt that the number of vertebrae between the anterior dorsal fin pterygiophore and the posterior anal fin pterygiophore had taxonomic significance. A comparison of this specimen with Recent *A. calva* showed that the vertebral count of this region is essentially the same in both species. This character is therefore not useful in distinguishing this species from the Recent form or in characterizing it as a specific taxon. The specimens of *A. scutata* are within the range of *A. calva* in total number of vertebrae as well as in the number of vertebrae in the various categories (Table 9). Based on the similarity of number of vertebrae in *A. scutata* to that of *A. calva,* it appears that the amiid vertebral column has not changed meristically from Oligocene to Recent.

Additional data from five undescribed fossil amiid specimens with relatively complete axial skeletons has been of considerable help in estimating vertebral counts of the fossil forms. A complete specimen of *A. uintaensis* from the Green River Formation (PU 13865) has a complete axial skeleton (Plate 3). Interestingly, the total number of centra (85) does not differ from that of *A. scutata* or *A. calva* (Table 9). The only variation is in the number of trunk centra and the number of diplospondylous caudal centra. There are fewer trunk centra in this specimen of *A. uintaensis* (31) than in *A. scutata,* which has a mean of 36, or in *A. calva,* whose trunk centra are a mean of 37. A partially complete *A. uintaensis* specimen (AMNH 785), also from the Green River Formation, shows almost the same number of diplospondylous caudal centra as PU 13865 (20–21 respectively). The lesser number of trunk centra in both specimens of *A. uintaensis* is thus offset by a greater number of diplospondylous caudal centra. In comparing the vertebral column of *A. uintaensis* with that of *A. calva, A. scutata,* and *A. fragosa,* it appears that although *A. uintaensis* shares the same total number of vertebral segments with *A. scutata* and *A. calva,* it does not conform to their proportional division of the column into trunk and caudal regions. *A. uintaensis* has a trunk/total-number vertebral ratio of 0.365, while *A. fragosa* has a ratio of 0.300 as compared to the *A. calva* ratio of 0.440. Three complete specimens referred to here as *A. fragosa* (*"Paramiatus gurleyi"* FMNH 2022, *A. kehreri* BMNH P33480, and *A. fragosa* MCZ 5341) have vertebral columns that differ proportionately and meristically from *A. calva, A. scutata,* and *A. uintaensis. A. fragosa* has significantly fewer centra than the other fossil forms, with approximately 12 fewer trunk vertebrae and 8 fewer monospondylous caudal centra. It has approximately the same number of diplospondylous caudal centra as *A. calva* and *A. scutata,* with the number of fused hypurals also essentially the same (Table 9). Thus *A. fragosa* and *A. uintaensis* are meristically distinct from one another and also from *A. scutata* and *A. calva,* suggesting that these two earlier forms can be taxonomically separated on vertebral meristic characters.

VERTEBRAL COLUMN OF *AMIA CALVA*

The existing taxonomy of many North American fossil amiids is based primarily on vertebral characters. Many of the species of *"Protamia,"* and the genus itself as described by Leidy (1873a) from the Bridger Formation, have been established solely on height/width proportions and length (thickness), shape of the neural and aortal facets, and various foramina of isolated vertebrae. Fossil species of *Amia* from the Bridger and Cypress Hills formations have also been defined on character-states of isolated vertebrae. In order to analyze this usage, variation in vertebral character-states of *A. calva* has been studied.

The axial skeleton of Recent *Amia calva* is relatively well known. It is one of the few modern forms that have diplospondylous vertebral centra posteriorly, a condition that, according to Schaeffer (1967), functionally increases the flexibility of the posterior part of the body. Shufeldt (1885) was one of the first to describe the vertebrae of *Amia,* and Hay's (1895) well-known work on the vertebral column of *Amia* provides a relatively complete and informative description of the axial skeleton, as well as one of the first discussions of intracolumnar variation of the centra. Hay observed some gradual changes in centrum proportions, and in the position of the neural and aortal facets.

Vertebral Features

Dorsal and ventral facets, basapophyses, foramina, and ridges on the centra have been used as diagnostic characters in the taxonomy of fossil amiids. There are three types of paired facets on the vertebrae: dorsal neural facets for the neural arches, ventral aortal facets for the aortal supports, and haemal facets for the haemal arches.

Neural facets. The neural facets are shallow depressions under the neural arch bases, which in life are filled with cartilage. Cartilage is present between the centrum and its associated neural arch. Some specimens of *A. calva* have much deeper facets, with a small ossified ridge built up on the borders. These neural facets occur in pairs on the dorsal surface of both trunk and caudal vertebrae, and between the two facets lies a groove that partially receives the spinal cord.

According to Hay (1895: 7–9), there is a marked anteroposterior change in the position of the neural facets. He contended that at the anteriormost end of the vertebral column the neural arch bases occur between two vertebrae and rest equally on

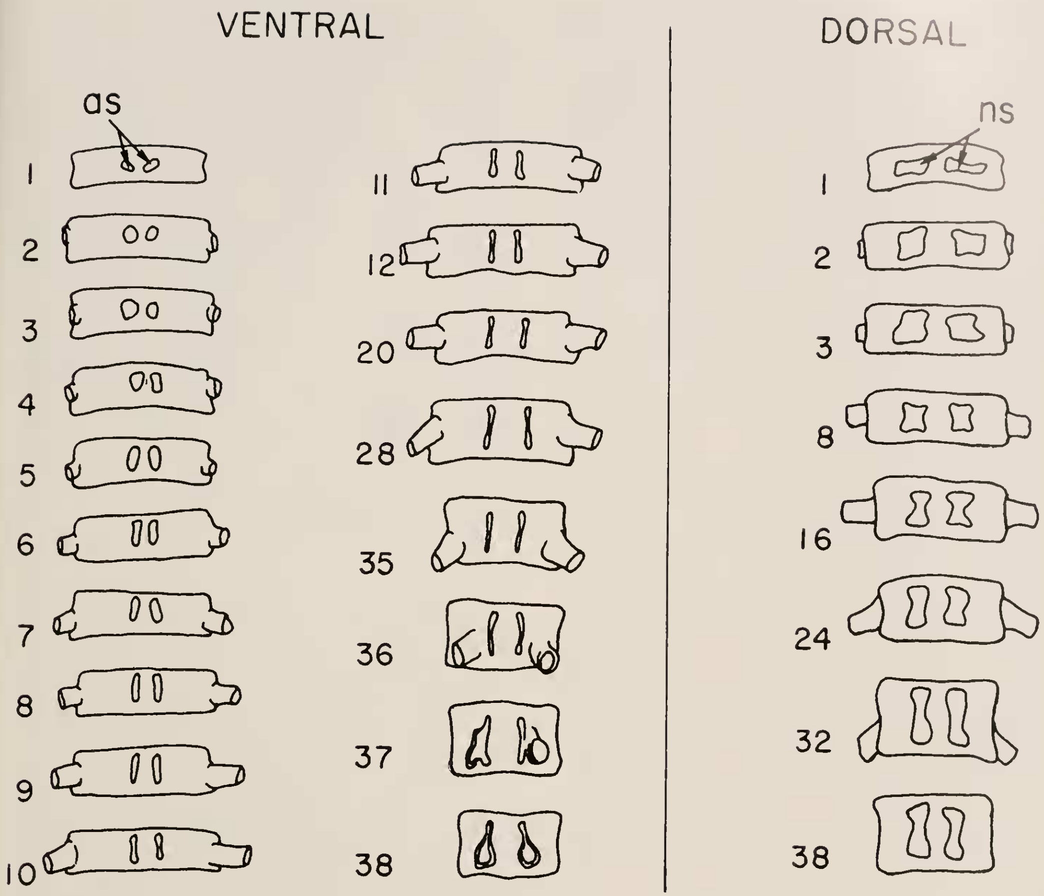


Fig. 11. Configuration of aortal facets (as) and neural facets (ns) on trunk and anterior caudal vertebrae of *Amia calva* (339 mm SL).

both; going posteriorly these bases shift gradually backward. He also observed that there is a change in the spacing of the neural arches; they are close together in the anterior trunk region and more widely spaced posteriorly. Hay is correct in regard to the change in spacing of the neural arches, but he is not altogether correct in his description of the change in position of these arches in relation to the centra. An examination of the Wisconsin *A. calva* sample showed that, after the first few anteriormost centra and corresponding neural arches, the middle of the neural arches is situated at the juncture between the centra. This placement continues along the axial column until the first diplospondylous vertebra occurs. At this point, the next five to seven neural arches are found aligned to the middle of each of the corresponding centra, after which the arches appear to move forward slightly and correspond irregularly to the vertebral bodies.

The configuration of the neural facets themselves varies in the trunk region of the vertebral column of *A. calva*. The neural arches in the anterior trunk region are thicker and wider than those in the more posterior trunk region which have become more flattened and elongated. The shape of the neural facets reflects this trend (Fig. 11). After the first two centra, the facets assume an hourglass shape, being narrower in the middle and broader at each end.

This can be related to the fact that the neural arches are situated at the juncture of two centra so that each neural facet supports the anterior and posterior halves of two different neural arches, whose bases are narrow at the extremity and thick in the center. Although the neural facets in any given specimen of *A. calva* conform to this general trend, the individual configuration of the facets varies slightly. Given this variation in shape of the neural facets, it is useless to attempt characterization of the vertebral column of any amiid species based on configuration of neural facets.

Aortal and haemal facets. On the ventral side of the trunk vertebrae are two thin cartilaginous projections that are located on either side of the dorsal aortal supports. When the skeleton is dried, these projections leave marked depressions, which, like the neural facets, vary gradually from the first anterior vertebra to the last few trunk vertebrae; at this point the aortal facets coalesce with the basapophyses (Fig. 11). The point where these two elements are completely merged marks the termination of the trunk centra, and the next centrum is that of the first caudal vertebra. These structures, which were derived anteriorly from the basapophyses and aortal facets, here become the haemal facets.

The first pair of aortal facets is very small and ovoid. The next few centra bear aortal facets that, as Hay (1895) also observed, are circular. The following aortal facets become successively elongated, until, with the tenth or twelfth vertebra, these facets have evolved into a long pair of slits, usually narrower at the midpoint. Posteriorly, these slitlike aortal facets remain basically the same shape until, at the end of the dorsal trunk region, they merge with the basapophyses to form haemal facets. Hay (1895: 54–57) states that the cartilaginous aortal supports penetrate deeply into the centra of younger individuals, while in older specimens they rest superficially on the centra. The aortal facets are deeper and more distinct than the neural facets.

Beginning with approximately the tenth or twelfth vertebra, the slit-shaped aortal facets are vertically situated on either side of an indentation that contains the aorta (Fig. 11). The first four centra have thicker and shorter supports with relatively little or no space between them. The aorta lies ventrally under the basioccipital, which bears aortal supports whose facets are of the same shape as the first four centra (Estes and Berberian, 1969, fig. 2B for *A. fragosa*). The aortal facets of the first eight vertebrae are different from all other trunk vertebrae, whose shape, as mentioned above, is basically an elongated slit. These aortal supports are thus helpful in distinguishing the first eight or so vertebrae from the remainder of the trunk centra in disarticulated specimens (Fig. 11).

Haemal facets. The haemal facets, which contain a cartilaginous layer between the centrum and the haemal arches, are nearly rectangular-shaped pairs that do not vary along the caudal portion of the vertebral column until the first fused urals. The furrow or indentation that lies between the aortal facets in the trunk centra continues in the caudal region between the paired haemal facets, although it gradually decreases in width and depth. Unlike the neural facets, the haemal facets are outlined by an ossified border, which can be helpful in distinguishing dorsal from ventral surfaces in disarticulated caudal vertebrae.

Since the ossified walls are tilted 20 degrees posteriorly to accommodate the haemal arches, which articulate with the cartilaginous layer diagonally rather than laterally, those borders are also useful in determining the anteroposterior orientation of the centrum.

Basapophyses. Amia trunk centra are distinguished from the caudal vertebrae by their having prominent paired processes, which have been called transverse processes, parapophyses, or diapophyses. I follow the terminology of Bolk *et al.* (1936), wherein they designate these structures, which are the processes for pleural ribs, as basapophyses ("basalstümpfe"). The first centrum often lacks these basapophyses

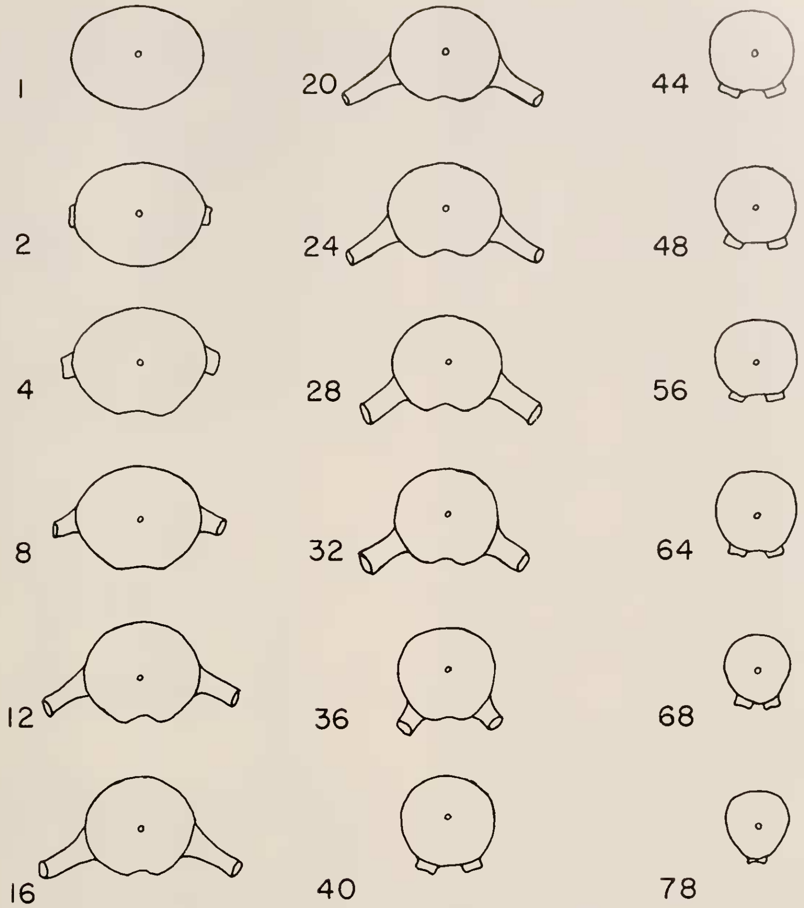


Fig. 12. Shape of selected trunk and caudal vertebrae in *Amia calva* (339 mm SL).

(Tables 10–12), which are always present on the succeeding centra and progressively become longer until approximately the twelfth (Fig. 12). The basapophyses are approximately the same length between the twelfth and the thirty-second centra, from which point they begin to diminish gradually in length until the last trunk centrum, where they coalesce with the aortal facets. The lengths of the basapophyses were not individually measured; this data would be of little practical use in a comparison of Recent and fossil material since these relatively fragile structures are rarely preserved intact in fossils. The distal end of each basapophysis is attached to a pleural rib by means of cartilage. The proximal ends of the basapophyses are ankylosed to the ventral half of the vertebral body. These paired processes are solid cylinders (hollow at the tips) that are slightly flattened dorsoventrally. Each pair of basapophyses may not always be of equal length or diameter, but they are extremely regular in position. They form two continuous and symmetrical lines that gradually come closer together until the last trunk centrum, where they are separated only by aortal supports.

An important aspect of the basapophyses in *A. calva* is the angle between each individual pair which gradually decreases posteriorly. Since the angle between the basapophyses is generally still available in fossil forms, even in those with broken basapophyses, it is used here as a basis of comparison between the Recent and fossil forms. Since the angles steadily decrease posteriorly along the vertebral column (Figs. 12, 14), they are also useful in orienting disarticulated centra to approximate position along the column. Although there is individual variation in these angles (Tables 10–12), they are nevertheless consistent enough to help in determining the general position in the column of any single trunk centrum. The range of angles extends from approximately 180 degrees anteriorly to 45 degrees posteriorly. Since the three *A. calva* specimens studied were of varying sizes (193 mm SL, 382 mm SL, and 423 mm SL), it would appear that there is no significant change in the angles with increasing size or age of the fish (Fig. 14). Although this transition is not perfectly linear, the angles are always decreasing posteriorly, and at least in the specimens I measured, there was never an instance of an angle's measurement being greater than that of the preceding centrum. The angle decrease occurs at a fairly constant rate until approximately the thirtieth trunk vertebra, at which point the rate of decrease of the angles is much accelerated (Fig. 14). The angle of the basapophyses is thus a reliable parameter in identifying the general position of isolated trunk centra.

Foramina, bone ridges, and first centrum. The trunk centra of *A. calva* have lateral foramina that, although lacking the uniformity of the neural and aortal facets, occur in irregular, distinct paired linear patterns. The foramina of the trunk and caudal vertebrae transmit numerous small blood vessels.

On the lateral surfaces perpendicular to the anterior and posterior articular surfaces of the individual centra are prominent bone ridges. These bone ridges add support to the arch anlagen, and also help unify the anlagen into a sturdy, functional vertebral body (Schaeffer, 1967). Externally, these bone ridges are not as regular as they are internally, although they still lie anteroposteriorly in the lateral and ventral regions and extend vertically along the basapophyses. They are also quite prominent in the notochordal furrow. Such bone ridges are not a unique feature of *A. calva,* and are common in teleosts.

The centra in *A. calva* are amphicoelous. The first four to six centra differ from all corresponding centra by having the anterior articular surface more convex than concave. The first centrum in nearly all specimens observed lacked basapophyses, and should therefore be considered a minor taxonomic character since first centra do occasionally occur with very small basapophyses. The

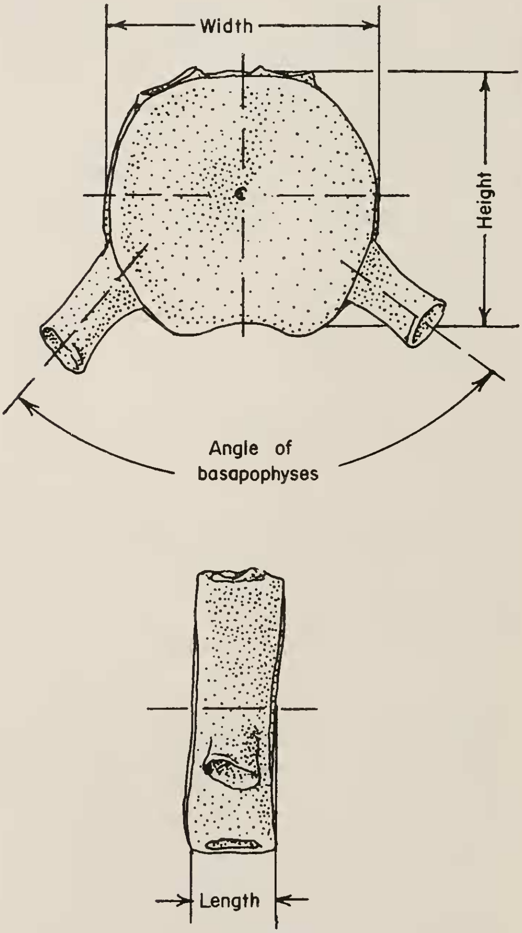


Fig. 13. Index to the measurements used, superimposed upon an outline drawing of an *Amia calva* vertebra.

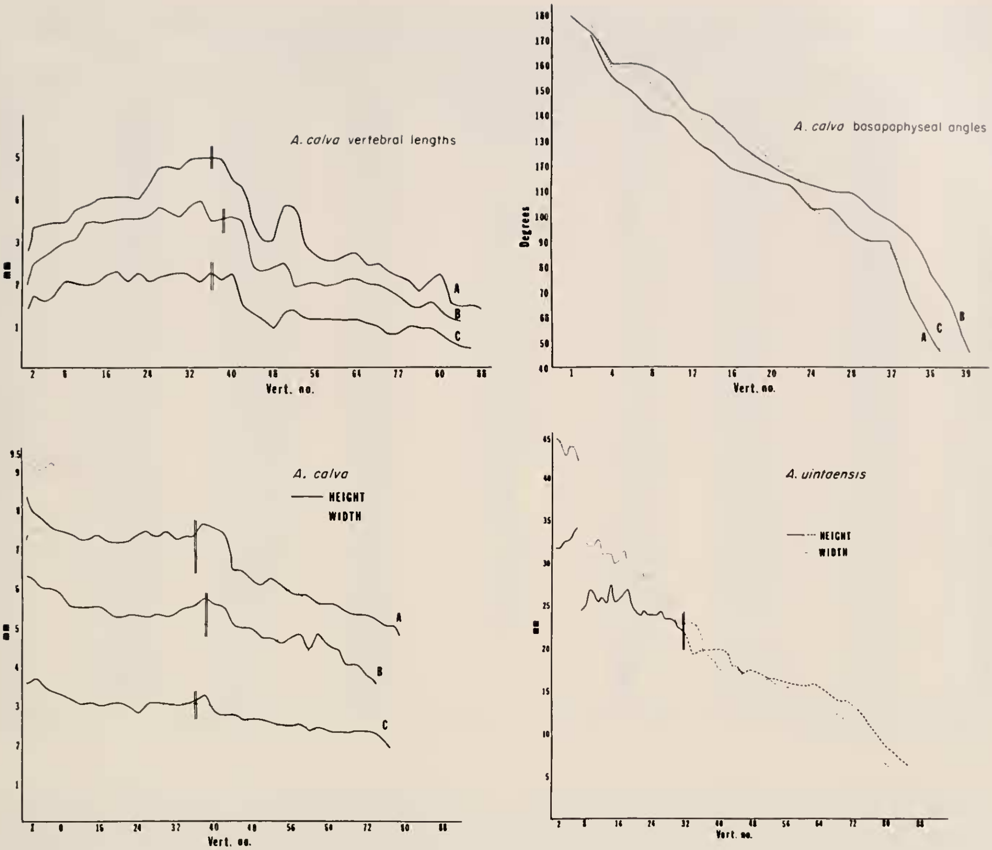


Fig. 14. Intracolumnar variation in the angle of basapophyses, length, height, and width of vertebrae in Recent *Amia calva* (A = 423 mm SL; B = 382 mm SL; C = 193 mm SL). Intracolumnar variation in height and width of trunk and caudal vertebrae in *A. uintaensis*. Vertebral column model based on first six centra from PU 10101 and fifty-nine centra from CM 25362; missing caudal centra have been interpolated and inferred based on PU 13865. The first anterior centra (PU 10101) were larger specimens and thus the anterior region of the trunk vertebral column model is "out-of-phase." Vertical lines = last trunk centrum.

ovoid shape of the aortal facets is a constant feature of all first four to six centra observed.

Vertebral Dimensions

A superficial but often-used character for diagnosing fossil amiid species has been the shape of the centrum. Descriptions for *Amia whiteavesiana, A. macrospondyla, A. exilis, A. elegans, A. depressus, A. newberrianus, Protamia symphysis, P. media, P. gracilis, P. uintaensis, P. plicatus, P. corsonii,* and *P. laevis* include centrum measurements for height, width, and length (thickness), as well as qualitative descriptions of the form and proportions of the centrum. Because isolated amiid vertebrae have often been the only anatomical material found in the fossil record, the original diagnoses were obviously limited in that a great deal of emphasis was placed on the vertebral centrum. In considering a single centrum shape as diagnostic for an amiid species, early authors implicitly assumed the vertebral column to be static, with no physical change or variation among the centra other than regional. Many new species were therefore described solely on variation in shape from other known amiid types.

TABLE 10. INTRACOLUMNAR VARIATION IN HEIGHT, WIDTH, LENGTH, AND ANGLE OF BASAPOPHYSES OF VERTEBRAE IN RECENT *Amia calva* (193 mm SL)

Vert. Cent.	Height (mm)	Width (mm)	Length (mm)	Angle of Basapophyses (Degrees)	Vert. Cent.	Height (mm)	Width (mm)	Length (mm)
1	3.55	4.35	1.40		44	2.75	2.75	1.35
2	3.65	4.20	1.70	176	46	2.60	2.65	1.15
4	3.70	4.25	1.65	159	48	2.65	2.65	.90
6	3.40	4.15	1.70	159	50	2.55	2.60	1.30
8	3.25	3.90	2.05	153	52	2.50	2.45	1.35
10	3.15	3.65	2.00	145	54	2.50	2.50	1.20
12	3.00	3.65	1.90	140	56	2.45	2.45	1.15
14	3.05	3.60	2.00	138	58	2.50	2.45	1.20
16	2.95	3.55	2.20	134	60	2.30	2.40	1.15
18	3.00	3.55	2.30	130	62	2.40	2.30	1.15
20	3.05	3.40	2.10	122	64	2.30	2.20	1.15
22	2.90	3.65	2.25	118	66	2.30	2.05	1.10
24	2.75	3.25	2.10	103	68	2.25	2.15	1.00
26	3.00	3.50	2.15	99	70	2.30	2.15	.80
28	3.05	3.35	2.20	93	72	2.30	2.10	.85
30	3.00	2.90	2.25	91	74	2.25	2.05	1.00
32	2.95	3.05	2.15	90	76	2.05	1.90	.90
34	3.00	3.00	2.05	74	77	1.87	1.75	.90
36	3.10	3.08	2.25	63	80		1.65	.80*
37	3.15	3.00	2.15	44	82		1.50	.68
38	3.25	3.00	2.10		84		1.25	.53
40	2.80	2.90	2.25		86		.80	.50
42	2.75	2.90	1.50					

* Fused.

TABLE 11. INTRACOLUMNAR VARIATION IN HEIGHT, WIDTH, LENGTH, AND ANGLE OF BASAPOPHYSES OF VERTEBRAE IN RECENT *Amia calva* (382 mm SL)

Vert. Cent.	Height (mm)	Width (mm)	Length (mm)	Angle of Basapophyses (Degrees)	Vert. Cent.	Height (mm)	Width (mm)	Length (mm)
1	6.30	7.21	1.90	180	42	5.50	5.05	3.50
2	6.25	7.41	2.45	173	44	5.15	4.65	2.40
4	6.00	7.50	2.50	161	46	5.00	4.80	2.35
6	5.95	7.25	2.85	161	48	4.90	4.60	2.37
8	5.82	7.10	2.95	159	50	4.70	4.45	2.50
10	5.56	6.90	3.05	154	52	4.70	4.45	1.90
12	5.50	6.65	3.45	143	54	4.65	4.55	2.00
14	5.50	6.25	3.45	140	56	4.70	4.45	2.10
16	5.50	6.25	3.45	133	58	4.80	4.10	1.90*
18	5.35	6.30	3.50	125	60	4.40	4.45	2.00
20	5.25	6.25	3.55	120	62	4.80	4.45	2.12*
22	5.30	6.25	3.55	116	64	4.50	4.10	2.12*
24	5.30	6.25	3.65	113	66	4.40	3.85	2.00
26	5.20	6.20	3.85	110	68	4.00	3.75	2.00
28	5.35	6.15	3.70	110	70	4.05	3.70	1.87
30	5.25	6.00	3.60	105	72	3.75	3.50	1.75
32	5.35	5.80	3.85	100	74	3.50	3.35	1.50
34	5.45	5.50	3.90	92	76	3.20	3.15	1.47
36	5.50	5.15	3.50	78	78		2.65	1.65
38	5.75	5.10	3.55	66	80		2.00	1.40
39	5.70	5.07	3.60	46	82		1.95	1.20
40	5.65	5.05	3.65		84		1.80	1.12

* Fused.

Table 12. Intracolumnar variation in height, width, length, and angle of basapophyses of vertebrae in recent *Amia calva* (423 mm SL)

Vert. Cent.	Height (mm)	Width (mm)	Length (mm)	Angle of Basapophyses (Degrees)	Vert. Cent.	Height (mm)	Width (mm)	Length (mm)
1	8.25	9.25	2.80		44	6.45	6.40	3.45
2	8.00	9.15	3.35	172	46	6.40	6.21	3.05
4	7.80	9.05	3.40	156	48	6.20	6.00	3.05
6	7.55	9.20	3.45	150	50	6.10	5.85	3.85
8	7.45	8.80	3.45	142	52	6.25	5.85	3.80
10	7.40	8.80	3.75	140	54	6.10	5.85	2.95
12	7.25	8.75	3.85	132	56	5.95	5.90	2.70
14	7.25	8.75	4.00	126	58	5.80	5.85	2.65
16	7.35	8.70	4.05	119	60	5.80	5.65	2.60
18	7.15	8.50	4.15	117	62	5.65	5.70	2.80
20	7.15	8.50	4.10	114	64	5.60	5.30	2.70
22	7.15	8.40	4.00	112	66	5.55	5.20	2.45
24	7.35	8.35	4.37	103	68	5.50	5.05	2.50
26	7.45	8.30	4.75	103	70	5.30	4.95	2.35
28	7.30	8.20	4.75	95	72	5.30	4.90	2.20
30	7.47	8.10	4.70	90	74	5.20	4.80	2.10
32	7.25	7.95	4.95	90	76	5.05	4.65	1.85
34	7.35	7.45	5.00	67	78	5.00	4.50	2.10*
36	7.35	6.90	5.00	52	80	4.75	4.45	2.25
37	7.50	6.70	4.95	46	82		4.15	1.55
38	7.65	6.50	4.90		84		3.25	1.50
40	7.60	6.50	4.50		86		2.50	1.50
42	7.40	6.20	4.35		88		2.00	1.45

* Fused.

One of the detailed studies on intracolumnar vertebral variation is Hoffstetter and Gasc's (1969) work on the vertebral column of snakes. Measuring individual centra in sequence, they plotted this variation; similar graphs are used here (Fig. 14). Three specimens of *A. calva* (193 mm SL, 382 mm SL, and 423 mm SL) were dissected and the individual vertebral dimensions measured to determine vertebral variation.

Length. Centrum length (thickness) was measured anteroposteriorly at the midline, above the basapophyses (Fig. 13). It was necessary to establish such a control for this measurement because of the variation in thickness within each centrum. In the trunk region, the centra are thickest ventrally at the neural and dorsal facets. The caudal vertebrae follow a similar pattern, being slightly thicker ventrally and dorsally, and thinner laterally. Every second centrum was measured for length (Tables 10–12). There is a distinct intracolumnar variation for this measurement, although the difference in length between consecutive vertebrae is usually small. There is also a general, if somewhat irregular, pattern in centrum length in *A. calva* (Fig. 14). The first two or three vertebrae of each *A. calva* specimen are relatively thin. These are followed by centra that gradually increase in length until approximately the last trunk centrum at the midbody. At this point there is a general trend again towards thinner vertebrae, although this pattern is erratic, particularly between the fiftieth and the fifty-fourth centra, where the thickness is suddenly increased and then decreases. This sudden change here in vertebral thickness occurs directly above the midline of the anal fin. The shortest vertebrae are the fused urals.

Height. Centrum height was taken dorsoventrally at the midline, between the aortal and neural facets (Fig. 13). Every second centrum was measured up to the fused urals, in which an accurate measure-

Table 13. Intracolumnar variation in height, width, length, and angle of basapophyses of vertebrae in *Amia uintaensis* CM 25362

Vert. Cent.	Height (mm)	Width (mm)	Length (mm)	Angle of Basapophyses (Degrees)	Vert. Cent.	Height (mm)	Width (mm)	Length (mm)
7	24.5	32.8	9.8	179	37	19.5	19.5	7.5
8	25.0	32.5	9.8	178	38	19.8	18.8	7.0
9	26.8	32.0	9.5	177	39	19.8	18.5	6.9
10	26.5	32.1	9.5	176	40	20.0	17.5	6.5
11	25.5	32.8	9.0	174	41	—	—	6.5
12	26.0	31.0	9.1	172	42	19.5	18.0	6.5
13	25.4	31.1	9.5	164	43	18.5	17.5	6.0
14	27.5	31.0	9.5	160	44	18.5	17.5	6.2
15	25.5	30.0	10.0	156.5	45	17.5	17.5	6.0
16	26.0	30.5	9.8	154	46	17.2	16.0	6.0
17	26.5	31.5	9.5	153	47	17.0	16.0	6.0
18	27.0	30.5	9.8	149	48	16.5	16.0	5.5
19	25.1	29.5	9.5	143	49	16.5	—	6.0
20	24.5	29.5	9.5	132	50	16.2	15.5	5.5
21	24.0	30.0	9.5	122	51	16.0	15.0	5.8
22	24.5	28.2	9.0	117	52	16.0	15.5	5.0
23	24.0	29.0	9.5	110	53	15.5	14.0	5.5
24	24.0	28.5	9.0	102	54	15.2	14.5	5.2
25	24.0	26.5	8.5	102	55	15.5	13.2	6.0
26	24.5	27.0	10.0	97	56	15.0	12.2	5.5
27	23.5	25.0	11.0	90	57	14.5	12.0	6.5
28	23.5	25.0	11.0	83	58	14.5	12.5	5.5
29	23.2	25.0	12.0	80	59	14.0	11.5	5.2
30	23.0	22.5	11.0	62	60	14.0	—	5.0
31	25.0	22.5	11.0	46	61	13.5	11.5	5.0
32	—	—	11.0		62	13.5	10.5	4.5
33	—	—	10.0		63	—	—	4.5
34	23.0	19.5	9.5		64	12.0	9.0	4.5
35	22.5	—	9.5		65	8.5	7.0	4.2
36	21.0	20.0	7.5					

ment would be obscured by the fusion of the hypurals. This series of measurements shows a basic pattern that is similar for each of the individuals studied, although there is less intracolumnar variation in the height than in the length measurements (Tables 10–12). The greatest height generally occurs at the anteriormost region of the column, then decreases slightly until the midtrunk region (Fig. 14). At this point the height gradually increases until it peaks at the end of the trunk region and the beginning of the caudal section, after which it decreases again toward the caudal region (Fig. 14).

Width. The width measurements were taken perpendicular to the height measurements, at the widest section of the centrum (Fig. 13). This dimension has a greater linear slope than the length and height dimensions (Fig. 14), which follow a more bell-shaped curve. There is a greater variation within the vertebral column for width dimensions (Fig. 14), as comparison of the height and width slopes reveals. The greatest intracolumnar width is always at the anteriormost portion of the trunk region, after which this dimension gradually decreases. There appear to be two areas where the rate of decrease is greater, these being at the terminus of the trunk region and at the first fused ural.

Height/width ratio. The centrum height/width ratio has been a commonly used diagnostic character in amiid taxonomy. Hay (1895: 7) correctly noted that the trunk vertebrae are somewhat broader than high (Fig. 14), and at the terminus of the trunk region the centra are nearly circular. The proportions tend to be reversed in the caudal region, however, with the height generally exceeding the width, although to a lesser degree than the proportional difference in the trunk region. The basic trend in shape through the vertebral column is thus a marked horizontally elliptical centrum approaching a progressively circular one, which then again becomes slightly vertically elliptical. Thus there is quite a variation in the centrum shape throughout the axial column, so that no one shape or ratio of dimensions could reasonably be considered diagnostic for all the centra of the vertebral column.

VALID NORTH AMERICAN FOSSIL GENERA AND SPECIES

Amia fragosa (Jordan, 1927)

Kindleia fragosa Jordan, 1927: 145.
Stylomyleodon lacus Russell, 1928a: 103.
Paramiatus gurleyi Romer and Fryxell, 1928: 519.

Holotype. NMC 8533e, anterior portion of right dentary.

Paratypes. NMC 8534a–d, f–n. (a), left operculum fragment; (b), cranial fragment; (c), anterior portion of left dentary; (d), anterior portion of right dentary; (f–g), coronoid with two styliform teeth preserved; (h–i), vomer without teeth preserved; (j), styliform tooth fragment; (k–l), posterior portion of right dentary; (m), left maxilla; (n), anterior portion of right dentary.

Type locality and horizon. Rumsey, Alberta. East half of section 31, T 34 S, R 21 W, Rumsey Quadrangle, Alberta; Edmonton Formation.

Age range. Campanian (Late Cretaceous) to Bridgerian (Middle Eocene).

Hypodigm. CRETACEOUS. Oldman Formation, Alberta: AMNH 5934, palatal fragments with styliform teeth; AMNH 5935, operculum and dentary. "Mesaverde" Formation, Wyoming: AMNH 5932, dentary and numerous coronoid teeth; AMNH 5933, vertebrae. Judith River Formation, Montana: AMNH 10109, left vomer bearing styliform teeth; AMNH 10110, dentary fragments, vertebrae, and skull elements. Edmonton Formation, Alberta: ROM 3064, coronoid teeth; ROM 3065, dentaries, vertebrae, and cranial fragments; UA 5398–5507, articulated and disarticulated specimens (see O'Brien, 1969 for identifications). Lance Formation, Wyoming: AMNH 9316, pterotic; AMNH 9315, operculum; CM 25363, dentaries; PU 17013, dentaries; UCMP 54013–54015, 54017, 54019, 54021–54030, 54035–54038, 54040–54056, 54059–54069, 54070–54120, 54141–54167, 54174–54180, 54188–54198, 54260, 54262, disarticulated elements (see Estes, 1964 for identifications). Hell Creek Formation, Montana: PU 17016, 17048, dentaries; PU 17014, coronoid teeth; PU 20554, dentary and vertebrae; MCZ 9286–9293, 9390–9432, 9559, disarticulated elements (see Estes and Berberian, 1969 for identifications).

PALEOCENE. Fort Union Formation, Wyoming: PU 17115, coronoid teeth; PU 17126, coronoid teeth and vertebrae; PU 17117, dentary and maxilla; PU 21525, portion of cranial roof with associated dentaries; PU 20523, dentary and coronoid teeth; PU 21174, vertebrae. Paskapoo Formation, Alberta: UA 131, dentary, numerous tooth plates, and vertebrae. Tongue River Formation, Montana: PU 20577, vertebrae, premaxillary fragment, and coronoid teeth; PU 20578, basioccipital and vertebrae; PU 17068, vertebra and dentary fragment. Melville Formation, Montana: AMNH 2635, cranial elements and associated dentaries. Tullock Formation, Montana: PU 17069, vomers.

EOCENE. Willwood Formation, Wyoming: MCZ 9264, nearly complete skull; PU 18780, tooth plate; PU 21175, dentary fragment and coronoid teeth; PU 16756, dentary and cranial fragments; PU 17649, anterior portion of skull; PU 21173, skull fragments and vertebrae; PU 13261–13262, cranial fragments and coronoid teeth. Golden Valley Formation, North Dakota: PU 18567, coronoid teeth and vertebrae. Wasatch Formation, Wyoming: PU 13260, tooth plates; PU 13259, cranial fragments and dentaries. Bridger Formation Wyo-

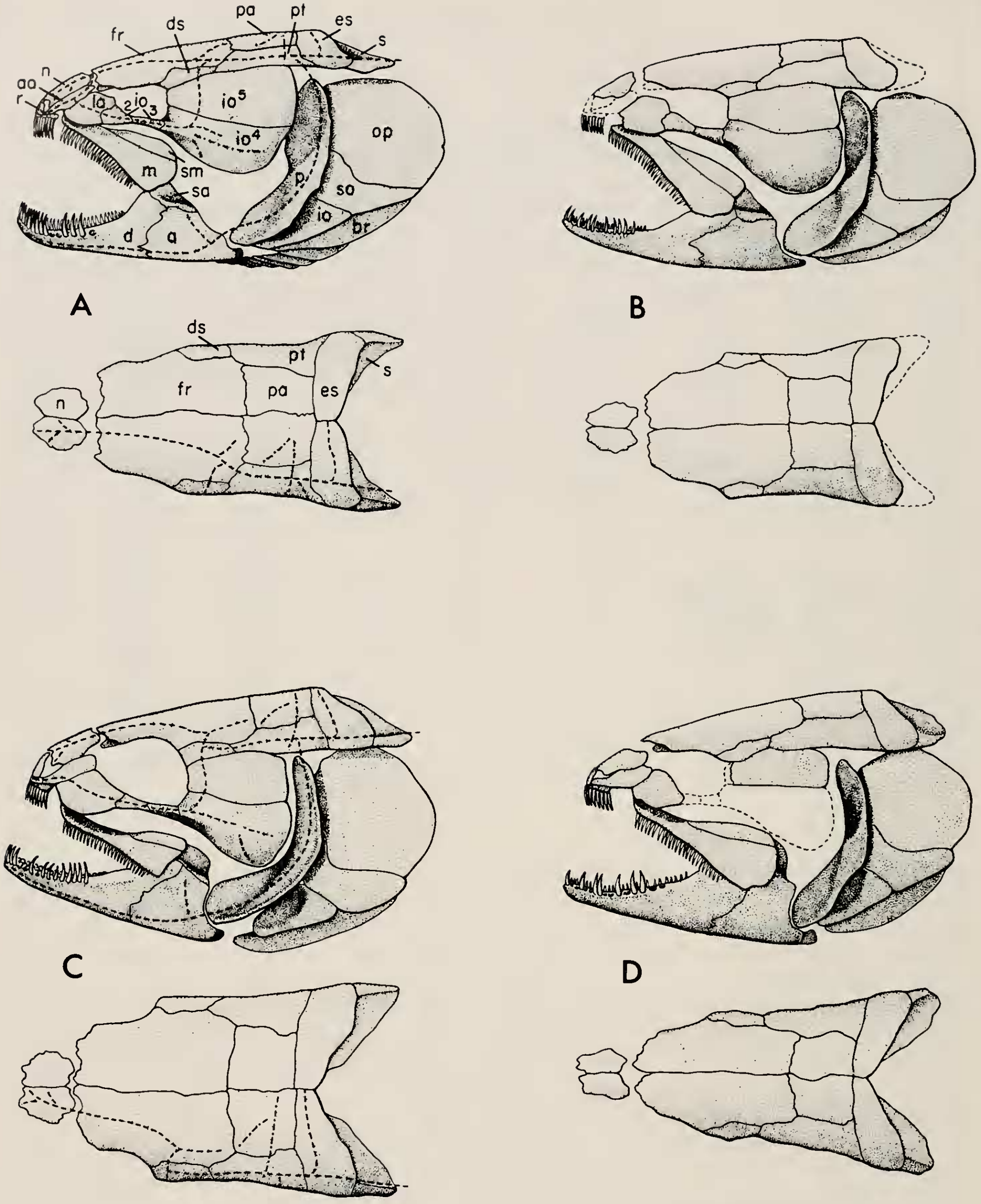


Fig. 15. A, *Amia calva*, Recent, Wisconsin; above, lateral, and below, dorsal views of skull. B, *Amia scutata*, Early and Middle Oligocene; above, lateral, and below, dorsal views of skull (sensory canal system and pit-lines are not known since skull elements are in articulation). C, *Amia fragosa*, Late Cretaceous to Middle Eocene; above, lateral, and below, dorsal views of skull (sensory canal system and pit-lines after Estes, 1964). D, *Amia uintaensis*, Paleocene to Early Oligocene; above, lateral, and below, dorsal views of skull (sensory canal system is only known in the mandible, operculum, nasal, lacrimal, antorbital, extrascapular, and suprascapular, all of which conform with those of *A. calva*).

Abbreviations: a, angular; ao, antorbital; br, branchiostegal rays; d, dentary; ds, dermosphenotic; es, extrascapular; fr, frontal; io, interoperculum; io^2 io^3 io^4 io^5, infraorbital series (suborbitals & postorbitals); la, lacrimal; m, maxilla; n, nasal; op, operculum; p, preoperculum; pa, parietal; pt, pterotic; r, rostral (ethmoid); s, suprascapular; sa, surangular; sm, supramaxilla; so, suboperculum. Dotted lines indicate the sensory canal system; dashed lines indicate pit-lines.

ming: YPM 6245, vomer and cranial fragments; YPM 6246, vertebrae; YPM 6247, dentary; YPM 6248, vertebra and cranial fragments; YPM 6254, vertebrae, basioccipital, vomer; YPM 6261, left operculum; ANSP 5630, vertebra. Green River Formation, Wyoming: MCZ 5341, FMNH 2201, complete specimens.

Known distribution. North Dakota, Wyoming, Montana, and Alberta.

Revised diagnosis. Vertebral column with significantly fewer total centra (65 mean) than the other species, with approximately twelve fewer trunk vertebrae (25 mean) and eight fewer monospondylous caudal centra (17 mean). Distance between anal fin insertion and the end of the vertebral column relatively short, with dorsal fin terminating close to caudal fin. Caudal lepidotrichia 19–20 rather than 23–27. Ascending processes of parasphenoid perpendicular to the main anteroposterior parasphenoid axis; more posterior placement of parasphenoid tooth-patch. Parietals squared in outline. Marginal teeth simple pointed cones, palatal teeth usually stout styliform crushers. Supraorbital sensory canal not entering parietal. Excavation of orbital notch in frontal relatively larger. Dentary with additional horizontal shelf of coronoid articulation surface adjacent to lingual border of alveolar ridge; coronoid articulation surface extensive, overlapping ventral half of ramus; dentary with pronounced arch rather than gradual curve in ventral outline. Greatest known standard-length 510 mm.

Introduction

Jordan (1927) described *Kindleia fragosa* as a new genus of cichlid fish from the Late Cretaceous Edmonton Formation of Alberta. This tentative placement of *Kindleia* within the Cichlidae was largely the result of his misinterpreting the splenial tooth plates for fused lower pharyngeal bones (Estes, 1964). One month later, Russell (1928a) independently published a description of *Stylomyleodon lacus*, a new fossil amiid from the Late Paleocene Paskapoo Formation of Alberta, and referred other specimens from the Edmonton Formation of Alberta to the same species. His description also included a dentary and palatal teeth modified for crushing. His relegation of the genus to the Amiidae was based on a correct interpretation of the "splenial" (=coronoid) tooth plates (Estes, 1964). He suggested a relationship of *Stylomyleodon* to *Platacodon nanus* (at that time erroneously considered an amiid; see Estes, 1964) with the essential difference being hemispherical rather than flattened tooth crowns.

Jordan later (1928) noted the similarity of the two genera *Kindleia* and *Stylomyleodon* and asserted the prior claim of his name *Kindleia*. Although he made no comment on Russell's attributing *Stylomyleodon* to the Amiidae, he rejected Russell's comparison of that genus with *Platacodon* on the basis of Marsh's earlier conviction that the latter was mammalian. In reply to Jordan, Russell (1928b) defended the validity of his genus on the supposition that its dentary was distinct from that of *Kindleia,* although he did agree on the similarity of teeth and jaw fragments of the two genera. Russell (1929) further attempted to validate *Stylomyleodon* as a genus by comparing his type with new specimens collected by Princeton University. This new material confirmed his association of the maxilla-dentary and palatine-coronoid dentitions, and also substantiated his interpretation of *Stylomyleodon* as an amiid in which the coronoid teeth were specialized for crushing. He also admitted that there was insufficient *Platacodon* material to determine any conclusive similarities with *Stylomyleodon,* but, referring to Hatcher's (1900, 1901) work, did insist that *Platacodon* was a fish. Simpson (1937) reported finding additional specimens of *Stylomyleodon* Russell in the Fort Union Formation at Crazy Mountain Field sites of Montana.

Estes (1964), from his studies of amiid material from the Lance Formation of Wyoming, observed that whereas the type dentary referred by Russell to *Stylomyleo-*

don was the posterior portion of an amiid dentary, Jordon's type was the anterior portion. From this fact he confirmed the synonymy of *Stylomyleodon* with the genus *Kindleia,* at that time believing that it was generically separated from *Amia.* Janot (1967) agreed with Estes on the synonymy of *Stylomyleodon* with *Kindleia,* but did not find sufficient cause to distinguish *Kindleia* generically from *Amia.* Russell (1967) continued to leave the nomenclatural problem of *Stylomyleodon-Kindleia* unsettled. Estes and Berberian (1969) studied material from the Late Cretaceous Hell Creek Formation of Montana and confirmed Janot's proposition that *Kindleia* is a synonym of *Amia.* They also suggested the possibility of synonymy of *A. fragosa* with *A. kehreri* (Middle Eocene, Germany), *A. russelli* (Late Paleocene, France), *A. munieri* (Early Oligocene, France), and *Paramiatus gurleyi* (Early Eocene, Wyoming), but postponed formal synonymy of *A. fragosa* with the prior name *A. kehreri* (Andreae, 1892), pending more detailed study of Early and Middle Cenozoic specimens from Europe. Estes and Berberian (1969: 10) concluded that the minor variations that separated *A. fragosa* and its related forms in Europe from *A. calva* are "superficial and essentially primitive," and indicated that the group might be close to the ancestry of the Recent species *A. calva.*

A nearly complete skull from the Eocene Willwood Formation of Wyoming (Fig. 16), two axial skeletons from the Eocene Green River Formation of Wyoming (Plate 1), and a sample of disarticulated elements from the Late Cretaceous, Paleocene, and Early Eocene have yielded more information on the osteology of *Amia fragosa.* Estes (1964), O'Brien (1969), and Estes and Berberian (1969) have studied this species in detail, and I therefore discuss these specimens only as they modify conclusions reached by those studies.

Fossil Record

In addition to the stratigraphic list given by Estes and Berberian (1969: 14, table 1) of major freshwater deposits carrying *A. fragosa,* three new localities are recorded here: the Late Paleocene Silver Coulee local fauna of the Fort Union Formation, Wyoming, and the Early Eocene Willwood and Wind River formations, Wyoming. The major deposits in which remains of *A. fragosa* have been found are summarized in Table 18. Estes and Berberian (1969: 10) state that the stratigraphic range of *A. fragosa* extends from the Late Cretaceous through at least Middle Eocene time in North America. The earliest deposit in which remains of *A. fragosa* have been found is the Late Cretaceous (Campanian) Oldman Formation of Alberta, and the latest deposit is the Middle Eocene (Bridgerian) Bridger Formation of Wyoming.

Cavender (1968: 128), however, describes *Amia* scales from the Late Eocene (Duchesnean) Clarno Formation of Oregon. Although these small scales (approximately 2 mm in length) are not as robust as those of *A. fragosa,* they are more ossified than *A. scutata* and *A. calva* scales. These scales, along with the scales from the Horsefly River Beds of British Columbia (UMMP collections) cannot at present be identified as to species. They are best referable to *Amia* sp., since no identifiable *A. fragosa* elements have been found later than Bridgerian and no specific character-states for scales of *Amia* have yet been determined.

Description

Neurocranium. Estes (1964: 29) stated that the greater length of the basioccipital and the presence of a second pair of aortal supports in *Amia calva* indicated that the basioccipital posterior to the spinal (intervertebral) arterial foramina included only one fused vertebra in *Amia fragosa* instead of the two found in *A. calva.* O'Brien (1969: 42) observed a similar condition in two complete *A. fragosa* specimens from the Edmonton Formation of Alberta. Estes and Berberian (1969: 2–3) found nine basioccipitals with one fused vertebra and eleven with two fused vertebrae from the

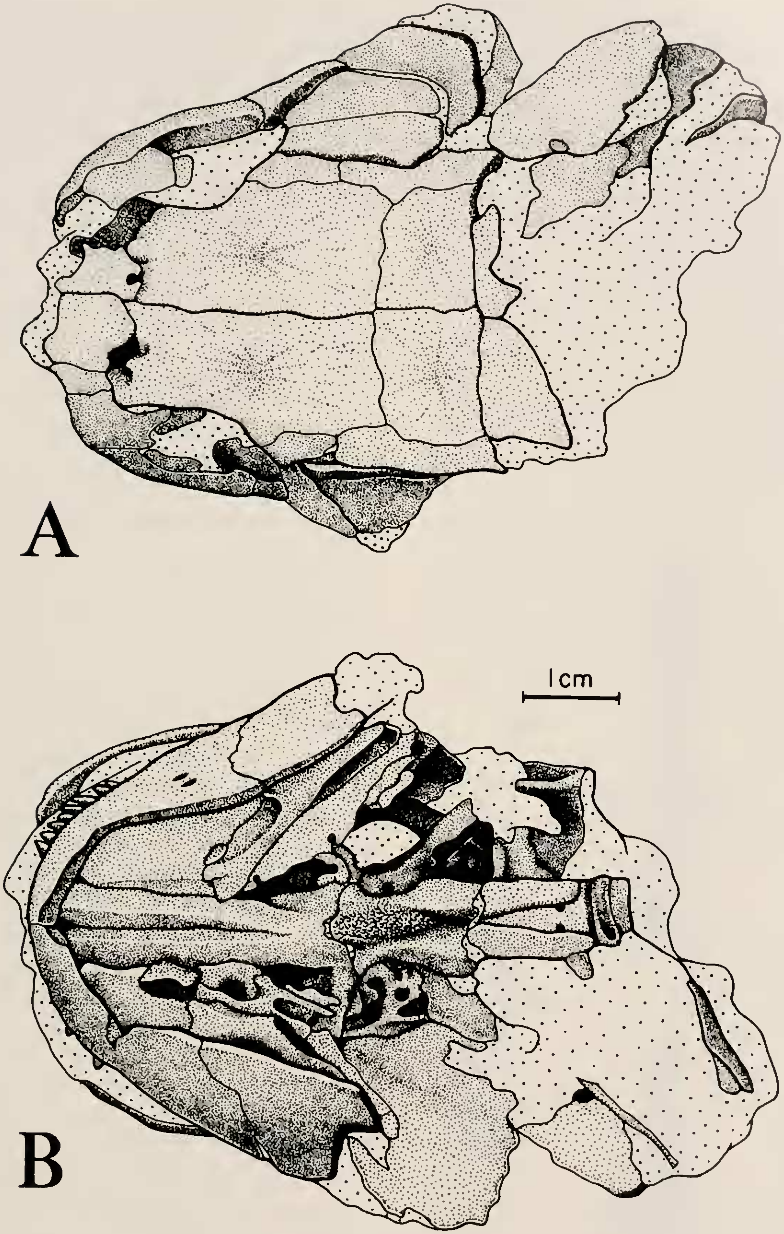


Fig. 16. *Amia fragosa* MCZ 9264, Early Eocene, Willwood Formation, Wyoming; A, dorsal; B, ventral.

Hell Creek Formation of Montana and interpreted this as a variation in *A. fragosa* not observed in the Lance sample. Janot (1967) noted that basioccipitals of the European Late Paleocene *Amia* sp. also showed this variation. Estes and Berberian (1969: 2) suggested that a weak tendency for fusion of vertebrae could be correlated with increasing size, and that such variation might possibly exist in the Recent species as well. Fifty Recent *A. calva* skeletons examined, with a size range of 100–480 mm SL, have the first two vertebrae fused to the basioccipital. Three articulated and twenty-two disarticulated Eocene and Oligocene *Amia uintaensis* basioccipitals all have two vertebrae fused to the basioccipital. Unfortunately, in specimens of *A. fragosa* (MCZ 9264, PU 13261) having a visible parasphenoid, the basioccipital regions are poorly preserved. There is a possibility that the Lance sample by chance contained only specimens with one fused vertebra since there are only six specimens known. Until more specimens of *A. fragosa* and *A. uintaensis* with intact basioccipitals become available, it is difficult to discuss this point further.

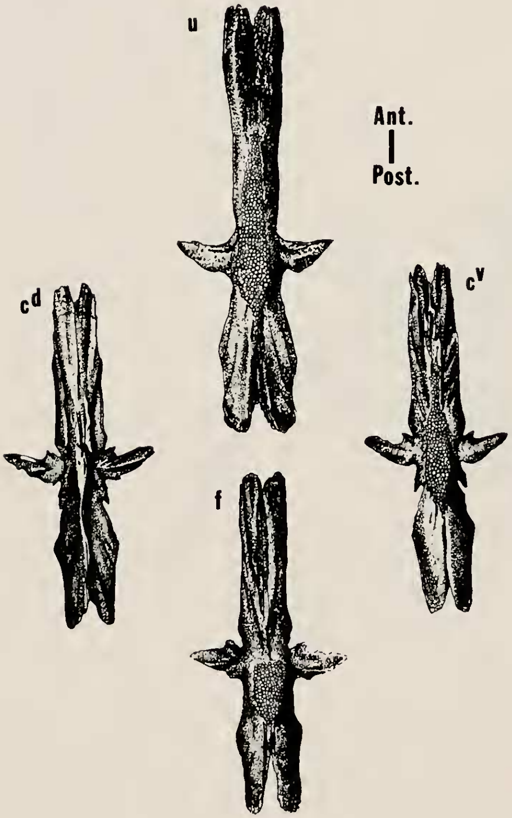


Fig. 17. Comparison of parasphenoids of *Amia* spp.: c, *Amia calva,* Recent, after Janot, 1967 (c^d = dorsal, c^v = ventral); f, *A. fragosa* (ventral); u, *A. uintaensis* (ventral).

The length of the *A. fragosa* parasphenoid posterior to the ascending processes is 10 percent shorter and slightly wider than in *A. calva,* with the ascending processes more posterior than in the Recent species (Fig. 17). The proportion of the length posterior to the processes to the length anterior to these processes (0.780) is not as small as in *A. uintaensis* (0.704) or as great as in *A. calva* (0.900), and, on the basis of this small sample, *A fragosa* is intermediate among the three species for this character. The region posterior to the processes also appears more convex than in *A. calva,* but not as convex as in *A. uintaensis.* The ascending processes are almost perpendicular to the main anteroposterior axis of the parasphenoid. Those of *A. fragosa* form an approximately 85-degree angle with the parasphenoid axis, while the ascending processes of both *A. calva* and *A. uintaensis* form approximately 70–75-degree angles. The mid-ventral surface of the parasphenoid bears small, sharp, conical teeth. This tooth-bearing surface of *A. fragosa* terminates anteriorly toward the middle of the ascending processes, whereas in *A. calva* this region narrows to a point and extends to the posterior end of the vomers (Fig. 17). In *A. uintaensis,* this region also extends to the vomers, but covers a wider surface area in the anterior region than in *A. calva.* Nearly all the tooth-bearing surface of *A. fragosa* lies in the posterior half of the parasphenoid, while in *A. calva* this surface is centered between the posterior and anterior areas; in *A. uintaensis* two-thirds of this surface lie in the anterior region of the parasphenoid. The entire tooth-bearing surface of *A. fragosa* is wider than that of *A. calva,* since the anterior half of the tooth-bearing surface tapers anteriorly in *A. calva,* while in *A. fragosa* the anterior portion maintains a more constant width. The basic outline of the tooth-bearing surface in *A. fragosa* is subrectangular; that of *A. calva* is more tear-drop shaped, with the anterior apex widened and extended to the vomers. The two posterior parasphenoid flanges are more splayed in *A. fragosa* than in *A. calva* or *A. uintaensis,* and overlie three-fourths of the basioccipital length. As Estes (1964: 29) notes, there is a relatively greater dorsoventral parasphenoid thickness in *A. fragosa* than in *A. calva.* The parasphenoid of *A. uintaensis* is proportionately more massive than that of *A. fragosa;* this massiveness, however, is probably a function of its greater size.

In *A. fragosa,* as in *A. uintaensis,* the extrascapular is tear-drop shaped, being narrow at the midline and expanded distally, while in *A. calva* and *A. scutata,* it is more strap-shaped and longer at the midline. The proximal anterior corner is squared off, as in *A. scutata* and *A. calva.* The anterior edge is distally concave at the pterotic-extrascapular suture, and the posterior edge is convex, particularly toward the distal end, which is straight rather than curved as in the other species of *Amia. A. fragosa* and *A. uintaensis* lack the posterolateral projection displayed in *A. calva.*

The suprascapular resembles that of *A. calva,* except that the distal edge is relatively straight, rather than incurved. The posterior border is also straight, while in *A. calva* there is generally a slight concavity in the middle of this edge; in *A. uintaensis* this border is convex.

The pterotic extends further anteriorly than in *A. calva,* but not to the extent that it does in *A. uintaensis* or *A. scutata.* The dermosphenotic-pterotic suture is directed posterolaterally in *A. fragosa* and anterolaterally in *A. uintaensis, A. scutata,* and *A. calva.* As in *A. uintaensis* and *A. scutata,* this bone in *A. fragosa* is narrower anteriorly than posteriorly, whereas in *A. calva* the widths of these ends are relatively equal.

The dermosphenotic in *A. fragosa* is about the same relative size as in the other species of *Amia.* The anterior angle that forms the posterior border of the orbit is slightly more pronounced than in *A. scutata* and *A. uintaensis,* and considerably more so than in *A. calva* (Fig. 28).

The parietal in *A. fragosa* is characteristically square, whereas in *A. calva, A. scutata,* and *A. uintaensis* it is longer than wide. The length of the parietal relative to that of the frontal is less than in *A. calva* and *A. scutata* and about the same as in *A. uintaensis.* The characteristic deep excavation in the frontal for the orbit is displayed in all available specimens of *A. fragosa.* This led Estes (1964: 36) to postulate the presence of supraorbital bones, but the articulated specimens figured by O'Brien (1969) show that this was not the case. As Figure 28 shows, the ratio of orbital depth to length is greater in *A. fragosa* than in the other *Amia* species. As noted in the preceding section on the cranial morphometrics of the Recent *A. calva,* it is difficult to assign a specific character-state of parietal/frontal proportions to any of the individual fossil *Amia* species because of the similarity in parietal/frontal proportions (Table 7). It is apparent, however, that the frontals of the earlier species *A. fragosa* and *A. uintaensis* are longer relative to parietal-length than in the mid-Tertiary *A. scutata* or Recent *A. calva.* This feature is useful in comparing *A. fragosa* with these two species, but ineffective in distinguishing it from *A. uintaensis.*

As Estes and Berberian (1969) noted, the nasal displays a bifurcation of the anterior border that is lacking in *A. calva.* The bifurcation is also present in *A. uintaensis,* and the bone has approximately the same outline and size relative to head size as the other forms. All available specimens of *A. fragosa* show that the nasals lie much closer to the frontals than in *A. calva, A. scutata,* or *A. uintaensis.* Although Estes (1964) states that the lacrimal conforms closely with that of *A. calva,* his restoration lacks the small posterior notch in *A. fragosa* which accommodates the anterior process of infraorbital 2. The lacrimal in *A. fragosa* is evenly tapered at the posterior end, and is anteroposteriorly longer than in other *Amia.* It is also more dorsoventrally convex than in *A. scutata* and *A. calva.*

As in *A. scutata,* infraorbital 4 in *A.*

fragosa is much more dorsoventrally expanded than in *A. calva,* with the anteroposterior length extending almost to the anterior edge of the preoperculum. Infraorbital 4 of *A. fragosa* and *A. scutata* is more concave at the dorsal edge, and much more convex ventrally. The pit-line marks extend further ventrad than is indicated in the reconstruction by Estes (1964).

Branchiocranium. In *A. fragosa,* the supramaxilla is relatively shorter than in *A. uintaensis, A. scutata,* and *A. calva,* with a greater curve in the maxillo-supramaxillary suture. The dorsoposterior corner in *A. fragosa* tends to be angular, as in *A. scutata,* whereas in *A. calva* and *A. uintaensis* it is more rounded. The supramaxilla is deeper and more truncated at the anterior end than in other species of *Amia.*

There is a dorsal shelf adjacent to the lingual border of the alveolar ridge which widens the anterodorsal surface of the dentary (Fig. 18). This shelf is lacking in *A. calva* and *A. uintaensis,* in which the coronoid articulation surface slopes directly downward from the alveolar ridge. This region of the lingual dentary surface underlying the coronoids extends more ventrad at the symphyseal edge than in *A. calva,* and distinctly overlaps the ventral part of the ramus. There is no such overlapping in *A. calva;* the dorsal and ventral halves of this region separate to form Meckel's groove. The anterodorsal section of the dentary in *A. uintaensis* overlaps the ventral half, but not to the extent that it does in *A. fragosa,* and as the coronoid articulation surface is thicker, this thickened area of bone forms the dorsal wall of Meckel's groove as in *A. calva* (Fig. 18). As Estes (1964: 36) noted, the coronoid teeth are styliform and extend almost to the ventral border of the ramus at the anterior end; in contrast, the coronoid teeth of *A. calva, A. scutata,* and *A. uintaensis* are pointed and the coronoids do not extend as far ventrally as in *A. fragosa.* The anterior half of the dentary length is more curved than in *A. calva, A. scutata,* and *A. uintaensis* (Fig. 18). This is displayed in the MCZ 9264 specimen (Fig. 16), in which this curve approximates a 120-degree angle at the midpoint of the alveolar ridge. The outline of the dentary differs from that of *A. calva* and *A. uintaensis* in that the anterior end maintains an almost constant width up to the sharp curve at the midpoint of the alveolar ridge, at which point it widens noticeably. When the outline and curvature of the anterior end of the dentary of *A. fragosa* are compared with those of other species, the resulting difference appears to be correlated with *A. fragosa's* relatively smaller mandible/head ratio (Table 7), smaller mouth gape, and its wider cranial roof (Fig. 15).

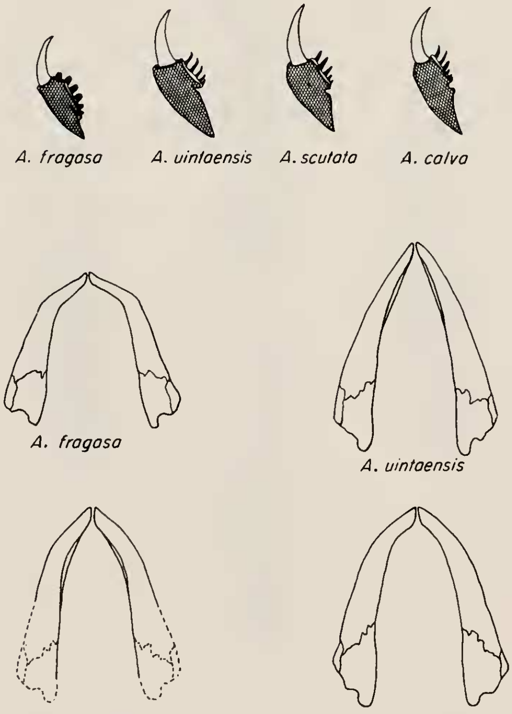


Fig. 18. Comparison of mandibles of *Amia* spp. (transverse sections and ventral views).

Post-cranial Skeleton. On the basis of specimens having only the lateral surface of the vertebral column exposed, it was concluded that centra of *A. fragosa* are indistinguishable from those of *A. scutata* and *A. calva.* Small disarticulated vertebrae are also basically similar in morphology, therefore it is impossible to differentiate *A. fragosa, A. scutata,* and *A. calva.* The midtrunk vertebrae of *A. fragosa, A. scutata,* and *A. calva* differ from *A. uintaensis* midtrunk vertebrae, which are generally larger, and subtriangular rather than ovoid. *A. fragosa* does, however, have a vertebral column that differs proportionately and meristically from that of other species (Fig. 31). It has a significantly smaller total number of centra than the other species, with approximately 12 fewer trunk vertebrae and 8 fewer monospondylous caudal centra. It has the same number of diplospondylous caudal centra as *A. calva* and *A. scutata;* the number of fused hypurals is also generally the same (Table 9). The low number of total vertebrae in *A. fragosa* is reflected by its shorter, deeper-bodied shape. The distance between the anal fin insertion and the end of the vertebral column is relatively shorter than in the other species. The dorsal fin also terminates closer to the caudal fin than in any of the other species of *Amia* (Plate 1; Estes and Berberian, 1969: 10). *A. fragosa* has fewer caudal lepidotrichia (19–20) than the other species of *Amia* (23–27). The head/standard-length ratio of *A. fragosa* is greater than that of *A. calva,* but is not significantly different from that of *A. uintaensis* or *A. scutata* (Table 3). The latter case is true despite the greater number of vertebral centra in *A. uintaensis* and *A. scutata;* this disparity may be explained largely by the fact that the *A. fragosa* skull itself is relatively shorter than that of the other two forms, particularly *A. uintaensis,* which has a greater head/standard-length ratio than *A. fragosa.* Thus head/standard-length does not significantly reflect the length of the vertebral column, but may be used as a character with this qualification in mind. The known total-length of *A. fragosa* falls within the range of *A. calva* and below that of *A. uintaensis* (Tables 1–2).

Discussion

Marsh (1871: 105) described *Amia newberrianus* and *Amia depressus* on the basis of disarticulated vertebrae and cranial elements from the Bridger Formation of Wyoming. His main criteria for distinguishing these forms from *A. calva* and from each other were that the chordal foramen of *A. newberrianus* was "considerably above the center in the dorsal vertebrae," and that *A. depressus* possessed broader vertebrae than *A. newberrianus* and lacked the median groove on the lower surface of the centra. The vertebrae indicated that both species were approximately the size of *A. calva.* Osborn *et al.* (1878: 102) noted that since Marsh gave no measurements, "the reference to *Amia depressus* cannot be certain." Marsh further noted that these specimens belonged to the Yale College Museum, but the specimens now seem to have been lost. Marsh had apparently assumed that the characteristics of one vertebra represented those of the entire vertebral column and was unaware of intracolumnar variation in height/width proportions, aortal facet morphology, and position of chordal foramen in the vertebral column of *Amia.* I infer from Marsh's report that the type specimen of *A. depressus* is probably a first to third trunk vertebra, since the aortal grooves are lacking (Fig. 11) and vertebral width exceeds height (Fig. 14). Using the position of chordal foramen as a character distinguishing *A. newberrianus* is undiagnostic since the position of the chordal foramen changes in relation to the relative position of the vertebra along the column (Fig. 12). Therefore, on the basis of Marsh's undiagnostic characters and the similarity in size and morphology of the vertebrae to those of *A. fragosa* and *A. calva,* I consider both *A. depressus* and *A. newberrianus* as *nomina dubia.*

Leidy (1873a: 98) described *Amia gracilis* from a single trunk vertebra, also from the Bridger Formation of Wyoming. He noted that the centrum has two "oblong fossae" (aortal facets) instead of the characteristic pair of ventral ridges found in *Amia calva.* The size of the centrum indicated to Leidy that *A. gracilis* was a smaller species than *A. calva* (Leidy, 1873b). The vertebra

(ANSP 5360) corresponds approximately to the twelfth trunk vertebra in *Amia,* since the aortal facets are oblong and unridged (Fig. 11). Although *A. gracilis* is small, it falls well within the size range of *A. fragosa* and *A. calva,* and is considered as a *nomen dubium.*

Estes and Berberian (1969: 10) suggested the possibility of synonymy of *Paramiatus gurleyi* (Plate 1) and *Amia fragosa* with the European *Amia kehreri* (Plate 2) on the basis of the close proximity of dorsal and caudal fins for the former and similarity of skull elements and teeth for the latter. It was shown in the previous section that *Paramiatus gurleyi* conforms not only to *A. kehreri,* but also to North American specimens of *A. fragosa* on the basis of body morphometrics and meristics. Cranial morphometrics were also shown to be similar. In addition, an X-ray (FMNH X2201) of the *Paramiatus gurleyi* skull reveals infraorbitals 4 and 5 to be longer than Romer and Fryxell (1928) and Estes (1964) had noted. The two infraorbitals extend posteriorly to the anterior edge of the preoperculum as they do in *A. fragosa* (UA 5398) from the Late Cretaceous Edmonton Formation of Alberta. The X-ray has also revealed a displaced left vomer with 26 styliform teeth which has been rotated through the skull roof and covered with matrix. All other cranial elements conform morphologically with other Cretaceous and Eocene specimens of *A. fragosa.* These additional similarities of *Paramiatus gurleyi* and *A. fragosa* confirm the synonymy of these two species which was suggested by Estes and Berberian (1969: 10), and I therefore include *Paramiatus gurleyi* in the synonymy of *Amia fragosa.*

Comments on Related European Forms

Amia kehreri was described by Andreae (1892, 1895) from a caudal region, infraorbital 4, disarticulated trunk vertebrae, and a left operculum from Middle Eocene (Lutetian) deposits at Messel bei Darmstadt (specimens at the University of Heidelberg, Andreae Collection). On the basis of specimens from the same deposit (BMNH P33480, Plate 2; P33488), it conforms morphometrically with *A. fragosa* in head/standard-length, pectoral fin insertion/standard-length, mandible/head-length, and operculum-length/operculum-depth (Tables 3, 7). The distance between the anal fin and the end of the vertebral column exceeds that of the North American *A. fragosa* specimens, but is less than in *A. scutata* or *A. calva.* The parietal/frontal ratio is also greater than in *A. fragosa,* but smaller than in *A. scutata* or *A. calva.* Meristics of vertebral elements as well as the cranial characters discussed by Estes and Berberian (1969) also conform with those of *A. fragosa.* I agree with Estes and Berberian (1969: 10) that only differences in temporal and geographical factors appear to distinguish *Amia kehreri* from *A. fragosa;* any osteological dissimilarities are of minor significance.

The Middle Eocene European Geiseltal deposits contain numerous amiid fossils; according to Estes and Berberian (1969) some showed resemblances to *A. kehreri.* This material is currently being described by Anna Jerzmánska, Uniwersytet Wrocławski, Wrocław, Poland.

Another related form is *Amia valenciennesi* from the Eocene of Puy-de-Dôme, France. Agassiz (1843) described the form from one complete specimen and an anterior region of another (BMNH P446, 27736). Piton (1940) reviewed these specimens along with new material collected at the same locality. *A. valenciennesi* also resembles *A. kehreri* in its vertebral number of 68 centra, close approximation of dorsal and caudal fins, and an infraorbital 4 larger than infraorbital 5; these similarities indicate that synonymy with *A. kehreri* is in order. The name *A. valenciennesi* precedes *A. kehreri,* and thus has priority.

Estes and Berberian (1969: 7) showed that *Amia russelli* Janot (1966, 1967) from the Late Paleocene of France resembles *A. fragosa* in (1) square parietals, (2) similar parietal/frontal ratio, (3) large orbital excavation in frontal, and (4) similar operculum height/width ratio. Thus *A. russelli* conforms with many of the most distinct characters of *A. kehreri* and *A. valenciennesi*, and should be considered a synonym of the latter.

Estes (1964) re-evaluated Dechaseaux's (1937) redescription of the Early Oligocene *Amia munieri* from France and noted similarities with *A. fragosa* which included (1) styliform vomerine teeth, (2) branchiostegal rays rounded distally, (3) larger infraorbital 4 than infraorbital 5, and (4) similar parietal/frontal proportions. The principal difference between the forms is the small excavation for orbits in *A. munieri*. Since Dechaseaux's and Estes' studies, the specimen (MNHN R4632, skull and associated cranial and postcranial elements) is being further prepared to display the cranial roof and palate more extensively. The frontal lacks a prominent excavation for the orbits as Estes (1964: 40) has noted, and in this feature *A. munieri* resembles *A. scutata* and *A. calva*. *A. munieri* is a very important form because it represents the only complete amiid specimen known from the Early Oligocene, and, as noted, it displays intermediate morphology of the cranial features among the species of *Amia*. *A. munieri* occurs very late in time in relation to the last known occurrence of *A. fragosa* in North America, and because there are no complete specimens known from this age, it represents a stage of evolution among the amiids that is not found in North America.

Lehman (1951) described *Pseudamia heintzi* (Tromsø Museum Naturhistorisk collections, Tromsø, Norway) from a fairly complete articulated specimen and two skulls from probable Eocene deposits in Spitzbergen. He differentiated this form from *Amia* on the basis of (1) *Sinamia*-like metapterygoid and (2) presence of a concave notch on the dorsoposterior border of the operculum. Estes (1964) noted that Lehman was incorrect in his interpretation of the nature of the metapterygoid and operculum, and therefore suggested that *Pseudamia* might be placed in the genus *Amia*. From the examination of Lehman's plates, it appears that this form resembles *A. fragosa* in its deep-bodied shape and low parietal/frontal ratio (approximately 0.410), and that it may be synonymous with *A. valenciennesi* and *A. kehreri*. Further preparation would possibly be helpful in uncovering palatal teeth, whose morphology would aid in a more definitive description. Although the exact age of the Eocene deposit in which the specimen occurred is uncertain, this Spitzbergen locality, if Early Eocene, lies on the possible migration route of amiids (and other vertebrates) between North America and Europe.

Amia uintaensis (Leidy, 1873)

Protamia uintaensis Leidy, 1873a: 98.
Protamia media Leidy, 1873a: 98.
Pappichthys plicatus Cope, 1873: 635.
Pappichthys sclerops Cope, 1873: 635.
Pappichthys laevis Cope, 1873: 636.
Pappichthys symphysis Cope, 1873: 636.
Pappichthys corsonii Cope, 1873: 636.
Pappichthys medius Cope, 1884: pl. 4.
Amia whiteavesiana Cope, 1891: 2.
Amia macrospondyla Cope, 1891: 2.

Holotype. ANSP 5558, anterior trunk vertebra.

Paratypes. ANSP 8044, first anterior trunk vertebra; ANSP 3151, three posterior trunk vertebrae; ANSP 5622, basioccipital.

Type locality and horizon. Henry's Fork. North half of section 5, T 12 N, R 111 W, Sweetwater County, Wyoming; Bridger Formation.

Age range. Torrejonian (Middle Paleocene) to Chadronian (Early Oligocene).

Hypodigm. PALEOCENE. Fort Union Formation, Wyoming and Montana: PU 17117, maxillary; PU 17068, vertebrae and dentaries; PU 16236, disarticulated skull and trunk vertebrae; CM 25364, dentary; PU 17064, trunk vertebrae. Tongue River Formation, Montana: PU 20578, basioccipital and vertebrae. Paskapoo Formation, Alberta: ROM 4653, vertebrae.

EOCENE. Willwood Formation, Wyoming: PU 21173, basioccipitals; PU 17227, basioccipital and trunk vertebrae; PU 17649, portion of cranium; PU 18760, skull fragments, dentary, and vertebrae. Wasatch Formation, Wyoming: AMNH 4635, dentary and maxilla. Golden Valley Formation, North Dakota: PU 18568, basioccipital. Green River Formation, Wyoming: USNM 18147, skull fragments and vertebrae; AMNH 785, complete caudal region; PU 13865, nearly complete specimen; MCZ 12916, disarticulated skull and associated vertebrae. Wind River Formation, Wyoming: AMNH 2437, dentary and skull fragments. Bridger Formation, Wyoming: CM 25362, portion of cranium and vertebral column; AMNH 4631, portion of cranium with dentaries, gular, and basioccipital; USNM 170976, maxilla; YPM 6238–6240, 6242, 6244, 6250–6253, 6257–6258, vertebrae and basioccipitals; USNM 170973, 5450, 3962, 3963, 3966, PU 20523, 10101, ANSP 2337–2339, vertebrae; USNM 2181, ANSP 5632, trunk vertebrae; USNM 3959, trunk and caudal vertebrae; ANSP 5580, mid-trunk vertebra; AMNH 2539, anterior portion of a left dentary, two premaxillae, right quadrate, left epihyal, anterior portion of an ectopterygoid, three trunk vertebrae, and numerous fragments of angular; USNM 3965, left dentary; USNM 3968, anterior dentary fragment; AMNH 2570, pre-maxillary fragment, fragments of angular, left quadrate fragment, trunk vertebra fragment, and a caudal vertebra; USNM 3960, PU 10099, 10110, vertebrae and a ural centrum; USNM 5476, basioccipital; USNM 3961, left dentary fragment. Washakie Formation, Wyoming: FMNH 27465, 4509, vertebrae. Uinta Formation, Utah: CM 2382, maxillary fragment.

OLIGOCENE. Cypress Hills Formation, Saskatchewan: NMC 6197, trunk vertebra; NMC 6198, caudal vertebra.

Known distribution. Montana, Wyoming, Utah, North Dakota, Alberta, and Saskatchewan.

Revised diagnosis. Vertebral column with approximately 20 more vertebral segments in total number (85) than *A. fragosa*, and five fewer trunk centra (31) and five more diplospondylous caudal vertebrae (21) than in the other long-bodied forms, *A. scutata* and *A. calva*. Mid-trunk vertebrae subtriangular rather than ovoid. Palatal teeth sharp, greatly curved inwardly. Between 40–45 vomerine teeth as compared with 15–17 in *A. fragosa, A. scutata,* and *A. calva*. Hyomandibular more deeply notched between opercular process and extensor (dorsal) surface than in other species; opercular process relatively larger. Angle between alveolar ridge and exterior surface of the dentary forms a more acute angle than in the other species. Mandibular ramus less curved than in other species, so that angle between symphyseal ends of dentaries is relatively narrow. Greater mandible/head ratio (0.693) and head/standard-length ratio (0.322) than any of the other forms: *A. uintaensis* has a head relatively longer and a mouth gape relatively wider than do other species. Most specimens are significantly larger than the other species, with a relatively greater degree of ossification of all bones. Greatest known standard-length 800 mm.

Introduction

Leidy (1873a) reported numerous disarticulated vertebrae of a fossil fish related to *Amia* from the Bridger Formation of Wyoming. He distinguished a new genus *Protamia* from *Amia* by its "two oval fossae" (aortal facets) on the ventral surface of the centrum, and by large vertebrae characteristically with a much greater width to height proportion. *Hypamia*, another new genus from the same locality which Leidy also related to *Amia*, was characterized by also being larger than *A. calva*, and by vertebrae whose sides converged into a "medium prominence excavated into a pair of oval fossae" deeper than those of *Protamia*. Later (1873b), Leidy published a more complete and illustrated account of the various species of the new genera *Protamia* and *Hypamia*. In the same year Cope (1873) described a new amiid genus, also from the Bridger Formation, which he named *Pappichthys*. He distinguished this new genus from *Amia* by the "presence of only one series of teeth, instead of several, on the bones about the mouth." Osborn *et al.* (1878) reported other finds of *Pappichthys* from the Bridger Formation which seemed to fit Cope's description. Cope (1884) further discussed his new genus, and rejected Leidy's prior nomenclature and description.

Newton (1899) discussed this nomenclatural controversy and asserted the validity of Leidy's genus *Protamia*, since Cope's later diagnosis was no more effective in characterizing the new genus than Leidy's prior one. Newton believed that Cope's description of *Pappichthys* as having only a single row of marginal teeth was taxonomically undiagnostic, since this condition would also include *A. calva*. Romer and Fryxell (1928) accepted Leidy's earlier description and genus as diagnostic, and referred *Pappichthys* to *Protamia*. They also mentioned *Hypamia* but found little to distinguish it from *Amia*.

Hussakof (1932) continued to use Cope's name, however, and reported large specimens of *Pappichthys* from the Eocene of Mongolia. He also noted Cope's error in diagnosing the tooth characteristics of the genus, since *Pappichthys* (*Protamia*) has several rows of small teeth on the "splenial bone." In comparison with *Amia* he noted "points of difference in nearly every bone available for comparison," and concluded that *Pappichthys* was a valid genus, "not merely a group of large-sized extinct species of *Amiatus*."

Estes (1964), like Romer and Fryxell (1928), referred *Pappichthys* to *Protamia*, and reported several vertebrae and a maxillary fragment from the Cretaceous Lance Formation of Wyoming. He interpreted the increase in breadth over thickness of the vertebrae as a possible "function of increased size," a condition that would also allow for the comparatively more massive nature of the maxillary fragment. He also considered the retention of this genus as arbitrary until enough materials were available. Janot (1967) did not consider this single distinguishing characteristic of the vertebrae as sufficient foundation for the erection of a new genus, and therefore suggested referring *Protamia* to *Amia*. Estes *et al.* (1969) concurred with Janot in synonymizing *Protamia* with *Amia*. The present study confirms this synonymy; Leidy's species (1873a) has priority and the valid name of this fish is thus the oldest specific name, *Amia uintaensis*.

Revision of all forms referred now or in the past to *Protamia* is much needed, for these large amiids were diagnosed on characters of isolated vertebrae and skull fragments. This study gives more useful diagnostic characters that provide a basis on which the taxonomy of this group can be established.

Fossil Record

The major deposits carrying remains of *Amia uintaensis* (Table 18) range in age from Middle Paleocene to Early Oligocene. Middle Paleocene specimens occur in the Fort Union, Tongue River, and Paskapoo formations and consist mostly of isolated and broken centra, and dentary and maxillary fragments. A nearly complete skull (PU 16236) with associated trunk and caudal centra from the Bear Creek local fauna of Montana (Fort Union Formation) is the only articulated specimen from the Late Paleocene. The Eocene material includes one complete articulated specimen (PU 13865), one complete caudal region (AMNH 785), and a disarticulated skull (MCZ 12916) from the Green River Formation. PU 13865 (Plate 3) has the axial skeleton intact in matrix, with a dislocated fifth centrum that is the only one available for three-dimensional measurements. This is also the only specimen in which a complete vertebral count can be taken. AMNH 785 provides excellent meristic information for the caudal region (Fig. 8C). CM 25362, from the Bridger Formation, consists of a left palatal and opercular series and an almost complete, disarticulated vertebral column that permitted the taking of a series of centrum measurements. Other skull fragments and vertebrae occur in many deposits throughout the Eocene (Table 18). The latest occurrence of *A. uintaensis* is represented by two isolated centra from the Cypress Hills Formation (Oligocene, Chadronian).

Description

Neurocranium. Posterior to the spinal arterial foramina the basioccipital includes two fused vertebrae. As the basioccipitals display great variation in the morphology of the articular surface, it is difficult to characterize this form on the basis of this feature. However, the articular surface is generally kidney-shaped, with dorsal indentations between the neural facets, and ventrally there is an indentation distal to the aortal facets. In *A. fragosa* and *A. calva* the basioccipital has ovoid articular surfaces with no dorsal indentations between the neural facets (Estes, 1964: 29, fig. 15). In lateral view the distal articular surface of the *A. uintaensis* basioccipital is not perpendicular to the parasphenoid flanges; the dorsal half of this surface is more anteriorly directed than the ventral half.

The parasphenoid is longer relative to its width than it is in either *A. calva* or *A. fragosa,* primarily in the region anterior to the ascending processes. At the point nearest the ascending processes, it lacks the pronounced convexity and the accompanying anterior lateral notches found in *A. calva* and *A. fragosa.* The ascending processes are slightly less anteriorly oriented in ventral view than in *A. calva,* but more so than in *A. fragosa* (Fig. 17). The region posterior to the ascending processes is relatively shorter than in *A. fragosa* or *A. calva;* it is also more massive and more ventrally convex than in the other two forms. The posterior parasphenoid flanges resemble those of *A. calva* more than *A. fragosa* in outline as well as juxtaposition; those of *A. fragosa* are more laterally splayed than in *A. uintaensis* or *A. calva.* The tooth-bearing surface differs considerably from that of *A. fragosa* and somewhat from *A. calva* in outline and extent. As in *A. calva,* this surface extends anteriorly to the vomers, but its width is much greater and more constant than in *A. calva,* which is narrowly tapered anteriorly. Posteriorly, this surface extends further than in *A. calva,* but not as far as in *A. fragosa.* Approximately two-thirds of the tooth-bearing surface lies anterior to the ascending processes, while in *A. calva* this area is anteroposteriorly centered, and in *A. fragosa* it is nearly all posterior. The tooth-bearing surface covers a greater portion of the ventral surface of the parasphenoid than in *A. fragosa* or *A. calva;* its basic outline is diamond-shaped, with the anterior apex widened and extended to the vomers, while that of *A. fragosa* is subrectangular and that of *A. calva* is tear-drop shaped with the apex sharply protracted anteriorly.

In *A. uintaensis* the distal edge of the suprascapular is convex as in *A. calva,* while in *A. fragosa* this edge is almost a straight line. The posterior border is more rounded distally than in *A. calva* and is convex rather than concave.

In having the extrascapular rounded at the distal border, *A. uintaensis* is the same as *A. calva* and *A. scutata,* but differs from both of them in that the posterior border is not concave, and from *A. calva* alone in lacking the distal posterior process. The anterior border is relatively straight, unlike the condition in *A. calva* and *A. scutata,* in which the lateral distal ends of the anterior borders are directly posteriad. As in *A. fragosa* the midline is shorter than in *A. scutata* and *A. calva.*

As in *A. scutata* and in *A. fragosa* the pterotic is narrower at the anterior than posterior border, while in *A. calva* and, to an extent, in *A. scutata* the ends are subequal. As in *A. fragosa* they extend farther anteriorly and adjoin the frontals posterolaterally. The dermosphenotic-pterotic suture is anterolaterally directed, as in *A. scutata,* but not as pronounced as in *A. calva.* The anterolateral edge of the pterotic is indented and forms, with the dermosphenotic, an additional concavity in the outline of the cranial roof. Aside from this anterior indentation, the lateral borders are relatively straight, as compared with the smoothly concave exterior sides of the pterotics in *A. scutata, A. calva*, and *A. fragosa*. The posterior border forms a smooth line, as in *A. fragosa*, and lacks the small lappet that *A. scutata* and *A. calva* display.

The dermosphenotic is similar to that of *A. calva* in relative size and outline, although it does not jut as deeply into the frontals. Its anterior border is rounded, as in *A. calva*, rather than sharply angular, as in *A. fragosa*. The posterior half of the outer lateral border is indented to form a concavity with the anterior tip of the pterotics. The parietal in *A. uintaensis* is elongated anteriorly, as in *A. calva* and *A. scutata*, while that of *A. fragosa* is relatively square. The orbital excavation in the lateral sides of the frontal is shallow as in *A. calva* and *A. scutata*, while that of *A. fragosa* is characteristically deep (Fig. 28). The sensory canal cannot be determined. The frontals are more elongated relative to parietal length than in *A. calva* and *A. scutata;* the parietal/frontal ratio is only slightly smaller than that of *A. fragosa* (Table 7). The distal lateral border tapers anteromedially, and the anterior ends are relatively pointed anteriorly, forming a deep notch on the midline suture.

There is a slight bifurcation of the anterior border of the nasal as in *A. fragosa*. The nasal bones are relatively narrower than in *A. fragosa* or *A. calva*, but are otherwise similar in shape and relative size. They are fairly well separated from the frontals, as in *A. calva* and *A. scutata*, rather than abutting them as in *A. fragosa*.

The lacrimal in *A. uintaensis* resembles that of *A. fragosa* in general morphology, although it lacks the posterior notch for the anterior end of infraorbital 2 which is present in the other species of *Amia*. The lacrimal, like that in *A. fragosa*, is relatively longer and more tapered posteriorly than in *A. scutata* and *A. calva*. It is more dorsally convex than in the other forms, but only slightly more so than in *A. fragosa*.

The infraorbital 5 in *A. uintaensis* is similar to that in *A. fragosa* and *A. scutata*, being less robust posteriorly than in *A. calva*. As in the other forms, it is narrower anteriorly than posteriorly. The ventral border is relatively straight, while that of the other forms is posteriorly convex. Infraorbitals 2, 3, and 4 have not been identified.

The vomerine tooth patch in *A. uintaensis*, as in *A. fragosa*, extends more posteriorly than in *A. calva* (Fig. 19). The vomerine teeth are sharp and greatly curved posteriorly; they exceed those of *A. fragosa* and *A. calva* in number, each vomer bearing between 40–50 teeth, as compared to half that number in *A. fragosa* and *A. calva*. The rostral and antorbital are identical to that of the other species.

Branchiocranium. The suture between the anterior and posterior dermopalatine cannot be discerned. In *A. uintaensis* the dermopalatine has about twice the number of teeth as in *A. calva*, and the tooth patch extends more distad. The teeth are sharply pointed, as are the vomerine teeth.

The hyomandibular is more deeply excavated between the opercular process and the extensor (dorsal) surface, and the opercular process is more massive and extends further ventrad, forming a larger articulation surface, as compared with the other species of *Amia*. The articular surface of the quadrate is more robust than in other species of *Amia* and displays three cristae ventrally rather than dorsally as in *A. calva* and *A. robusta* (Janot, 1967: 144). The ceratohyal resembles that of *A. calva* and *A. fragosa* with the exception of its being thicker at the neck of the proximal end. The metapterygoid in *A. uintaensis* conforms very closely to that of *A. calva* in outline and in the position of the anterior

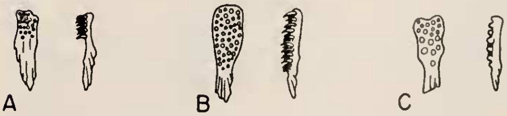


Fig. 19. Comparison of vomers of A, *Amia calva;* B, *A. uintaensis;* and C, *A. fragosa*.

basal process and the posterolateral otic process.

The maxilla in *A. uintaensis* is more robust and relatively longer, and its posterior border is dorsoventrally wider than in the other forms, particularly *A. fragosa.* As in *A. calva* the small supramaxillary notch occurs more anteriorly than in *A. fragosa.* The dorsoposterior border is rounded, as in *A. calva* and *A. scutata,* rather than sharply angular, as in *A. fragosa.* Anteriorly the maxilla is deeper and more thickly ossified than in the other forms, but this may be a function of greater size. The supramaxilla resembles that of *A. calva* in general morphology, being elongated and narrowly tapered anteriorly, with a smoothly rounded posterior end conforming to the curve of the maxilla. The maxillo-supramaxillary suture is straight as in *A. calva.* The premaxilla is identical to that of the other species.

The dentary of *A. uintaensis* is similar to that of *A. calva* and *A. scutata* in lacking the dorsal shelf of the anterior lingual border of the alveolar ridge which occurs in *A. fragosa.* The coronoids articulate more or less vertically on the alveolar ridge, as in *A. scutata* and *A. calva.* The anterodorsal region of the dentary slightly overlaps the ventral half, but not to the extent that it does in *A. fragosa; A. uintaensis* seems to be intermediate between *A. fragosa* and *A. calva* in this feature, the latter having no such ventral overlapping at the symphyseal edge. The coronoid articulation surface of the *A. uintaensis* dentary is thicker than in *A. fragosa* and *A. calva,* but only slightly more so than in *A. scutata.* At the termination of this surface, this thickened area of bone forms the dorsal wall of the Meckelian groove, as in *A. calva.* The ventral wall of this groove is less well defined than in *A. calva,* with *A. scutata* being intermediate. The anterior half of the dentary length in *A. uintaensis* is evenly tapered to the symphyseal edge; it is elongated and lacks the sharp curve present in *A. fragosa* at the midpoint of the alveolar ridge (Fig. 18). There is only a trace of such a curve in the dentaries of *A. calva* and *A. scutata* which are also more elongated and evenly tapered than in *A. fragosa,* although not to the extent that they are in *A. uintaensis.* Anteriorly, the bone is also relatively thicker than in *A. fragosa* and *A. calva; A. scutata* also displays this greater ossification at the anterior end of the dentary. Posteriorly, the dentary is very similar to that of *A. calva.* The coronoid teeth are sharp and conelike, extending to the midpoint of the lingual surface, as in *A. calva.* As Janot (1967) shows for *A. robusta,* the alveolar ridge is more horizontal in *A. uintaensis* and forms a more acute angle with the exterior surface of the dentary than it does in *A. fragosa* or *A. calva; A. scutata* is intermediate between *A. uintaensis* and *A. calva* in this feature (Fig. 18). In *A. uintaensis* the first coronoid (symphyseal) overlies only the dorsal half of the anterior articular surface of the dentary, as in *A. calva* and *A. scutata.* The teeth are more sharply pointed than in any of the other forms (Fig. 18). The second coronoid is fragmentary, but appears to resemble that of *A. calva* with the exception of its having more sharply pointed teeth. The prearticular specimens available are fragmentary, but the lingual surface possesses blunt-conical teeth similar to those in *A. calva* and *A. fragosa.* Dorsally, however, these teeth are as sharply pointed as the coronoid teeth. The angular is slightly longer and higher than that of *A. calva.* The posterior border is more vertical, with the articular notch less pronounced. It is more heavily ossified than in *A. calva,* but this may be a function of size. The surangular in *A. uintaensis* is basically similar to that of *A. calva,* although it is situated more dorsally and is more rounded at the dorsal edge.

The gular is longer than that of *A. calva* and *A. fragosa* (Fig. 20). It is also slightly narrower at the posterior end than the anterior end, while the reverse is generally true in *A. calva.* Otherwise, the gular strongly resembles that of *A. calva.* Despite a few minor dissimilarities, the preoperculum resembles that of *A. calva.* There is a

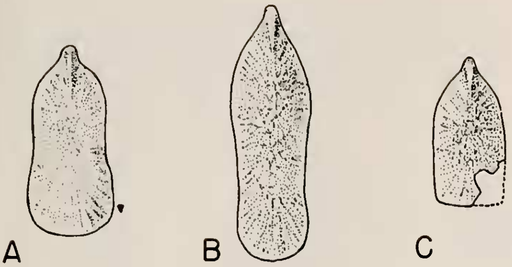


Fig. 20. Comparison of gulars of A, *Amia calva;* B, *A. uintaensis;* and C, *A. fragosa.*

slightly more pronounced concavity in the ventroposterior border than is exhibited in *A. calva;* this concavity is altogether lacking in *A. fragosa.* The line of curvature is about the same as in *A. calva;* in *A. fragosa* the preoperculum is more deeply curved. The dorsal half is not quite as wide as the ventral half, while in *A. calva* both ends are fairly equal. In *A. fragosa,* however, the dorsal half is much narrower and more tapered than the ventral half, which is relatively wider and bulbous. The operculum in *A. uintaensis* is similar to that of *A. calva* and *A. scutata* in operculum-depth/operculum-length (Table 7). The suboperculum conforms in general morphology with that of *A. calva,* although it is slightly more robust, particularly in the posterior region. The corners tend to be angular, as in *A. scutata* and *A. calva,* rather than rounded, as in *A. fragosa.* The interoperculum is similar to that of *A. calva,* although more robust. The anterodorsal border is more convex than in *A. calva,* and is more deeply impressed into the preoperculum. The anteroventral border is narrowly tapered as in *A. calva,* rather than smoothly rounded as in *A. fragosa.* The first branchiostegal ray conforms to that of the other species. Although the lack of articulated material makes any count of the rays difficult, in MCZ 12916 there are 12 disarticulated branchiostegal rays on the right side of the cranial roof. As in *A. fragosa* the distal ends of the rays are consistently rounded, rather than squared as in *A. calva.*

Post-cranial skeleton. The supracleithrum in *A. uintaensis* resembles that of *A. calva* and *A. fragosa,* excepting the dorsal articulation surface, which is rectilinear rather than pointed as in *A. calva.* The distal lateral border in the Paleocene specimens lacks the notch that occurs in *A. calva,* but this notch is present in the Eocene specimens. The metacleithrum in *A. uintaensis* is more elongated than in *A. calva* and *A. fragosa.* The dorsal end is narrower than in *A. calva,* and the ventral end is squared off. The cleithrum in *A. uintaensis* is largely similar to that of the other *Amia* species, but is more massive at the proximal end than in *A. calva,* and the dermal sculpture covers a greater area than in *A. calva,* extending to the distal border as in *A. fragosa* and *A. scutata* (Fig. 21). The mid-distal border is smoothly convex and lacks the notch ventral to the metacleithrum which is present in *A. calva.*

The preceding study of the vertebral skeleton of *A. calva* revealed changes in height/width proportions, position of chordal foramen, configuration of neural and aortal facets, and in the basapophyseal angles and length of basapophyses which may be used here to discern similar trends in *A. uintaensis* centra, for the fossil vertebrae display the same features characteristic of the Recent species even in disarticulated state.

CM 25362 from the Bridger Formation is the only specimen that has a relatively complete, disarticulated, undistorted verte-

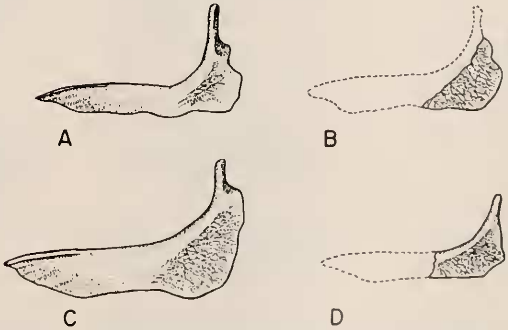


Fig. 21. Comparison of cleithra of A, *Amia calva;* B, *A. scutata;* C, *A. uintaensis;* and D, *A. fragosa.*

bral column; as the centra are separable this specimen is useful in comparisons with isolated vertebrae. There are 59 centra present: 25 trunk centra and 34 caudal centra, including two fused urals. Many of the preserved caudal centra are only fragments. Since the articulated specimen (PU 13865) has 85 vertebrae (see Table 9 for regional numbers) it may be assumed that about 25 vertebrae are missing from CM 25362. When comparing vertebrae from different regions of the column in the two specimens, it appears that CM 25362 lacks approximately six trunk and approximately twenty caudal centra. The first anterior trunk centrum present in the CM 25362 series possesses aortal facet configurations similar to those of the seventh vertebra of the articulated specimen (PU 13865). An articulated but separable series of six uncrushed anterior trunk vertebrae (PU 10101), also from the Bridger Formation, aids in the reconstruction of the anterior region of the *A. uintaensis* vertebral column (Figs. 22–25). The basapophyseal angles of these six PU 10101 vertebrae do not vary from 180 degrees. The first six anterior trunk vertebrae from a partly disarticulated vertebral column from the Paleocene specimen (PU 16236) resemble the six PU 10101 centra in length and shape of aortal facets, even though PU 16236 is a smaller individual. The height/width ratio of these latter centra is difficult to determine, however, since the specimen underwent postdepositional crushing. The nearly complete vertebral series of the CM 25362 specimen has been used for the construction of the remaining trunk and caudal region in the model of the *A. uintaensis* vertebral column. The trunk centra of CM 25362 have been arranged according to basapophyseal angles that decrease from 180 to 46 degrees, as in *A. calva*. Decreasing size was used to arrange the caudal vertebrae.

Although *A. uintaensis* occurs much ear-

TABLE 14. ANGLE OF BASAPOPHYSES, LENGTH, HEIGHT, AND WIDTH OF VERTEBRAE OF *Amia uintaensis* COMPARED WITH TYPE SPECIMENS OF SYNONYMIZED TAXA AS ILLUSTRATED IN FIGURE 22

Relative Vertebral Number	Specimen	Angle of Basapophyses (Degrees)	Length (mm)	Height (mm)	Width (mm)
1	*A. uintaensis* PU 10101	—	8.0	32.0	45.0
	A. uintaensis PU 16236		6.0	31.0	44.0
	P. uintaensis ANSP 8044		8.0	32.0	46.0
	P. sp. USNM 170973		5.5	19.0	29.0
2	*A. uintaensis* PU 10101	180°	8.0	32.0	44.5
	A. uintaensis PU 16236		8.5	28.5	39.0
	A. whiteavesiana NMC 6197		8.5	29.0	40.0
	P. sp. FMNH P27465		9.0	28.0	36.0
3	*A. uintaensis* PU 10101	180°	10.0	33.0	43.0
	A. uintaensis PU 16236		8.0	30.0	41.5
	P. sp. USNM 3966		8.5	21.5	29.0
	P. medius USNM 3959		8.5	22.0	30.0
4	*A. uintaensis* PU 10101	180°	10.0	33.0	44.0
	A. uintaensis PU 16236		7.5	33.0	40.8
5	*A. uintaensis* PU 10101	180°	11.0	33.5	44.0
	A. uintaensis PU 16236		9.5	31.5	39.0
	A. uintaensis PU 13865		4.5	16.5	21.5
6	*A. uintaensis* PU 10101	180°	11.0	34.0	42.5
	A. uintaensis PU 16236		9.0	33.5	34.0
	P. uintaensis ANSP 5558		10.5	32.5	40.0

lier in time than *A. calva* and *A. scutata,* it has approximately the same total number of centra (85), and like them is a longer-bodied form than its contemporary, *A. fragosa,* which has a mean of 65 centra. The vertebral column of *A. uintaensis* does,

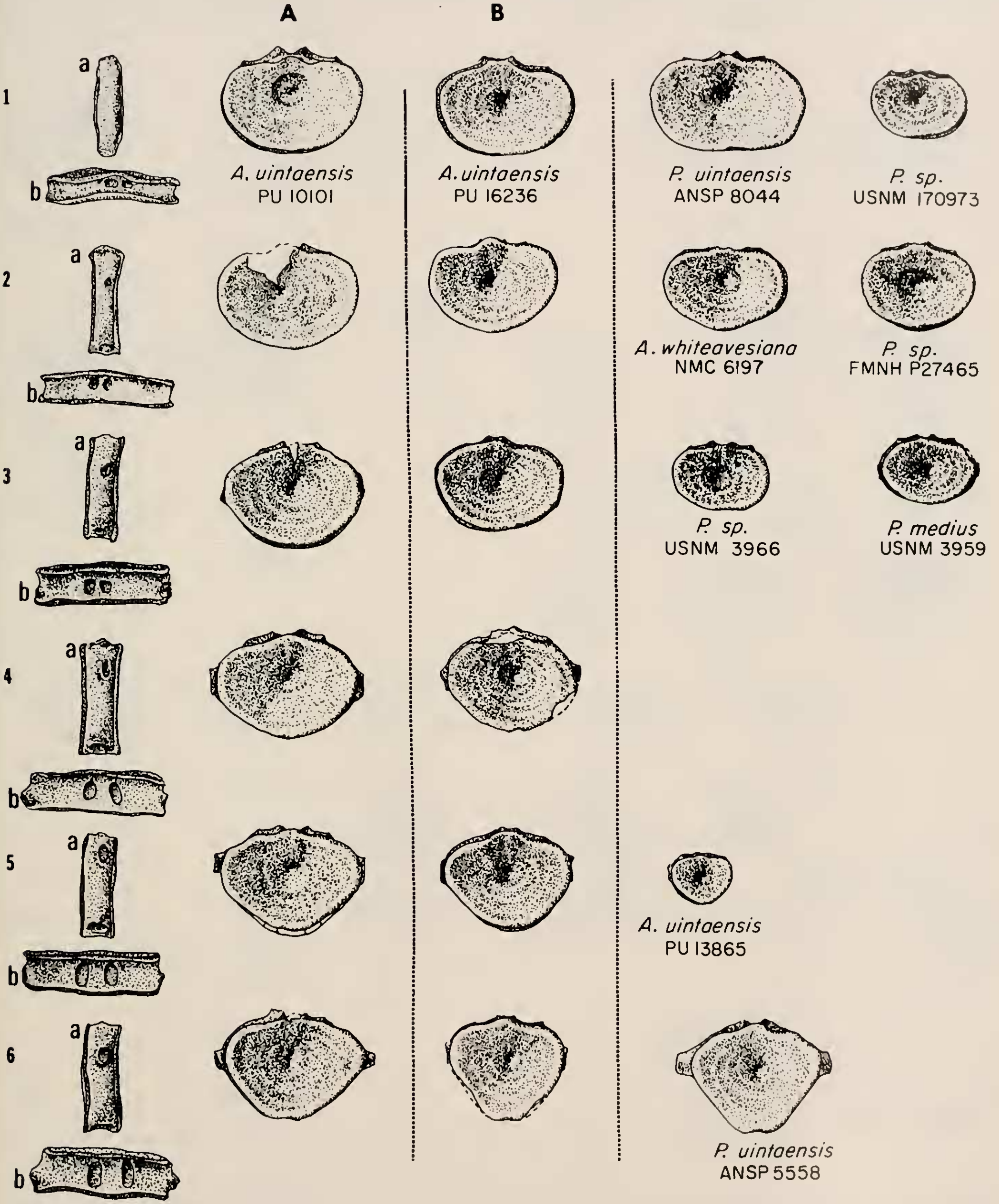


Fig. 22. First anterior trunk vertebrae (A,B) of *Amia uintaensis* compared with type specimens of synonymized taxa (refer to Table 14 for data).

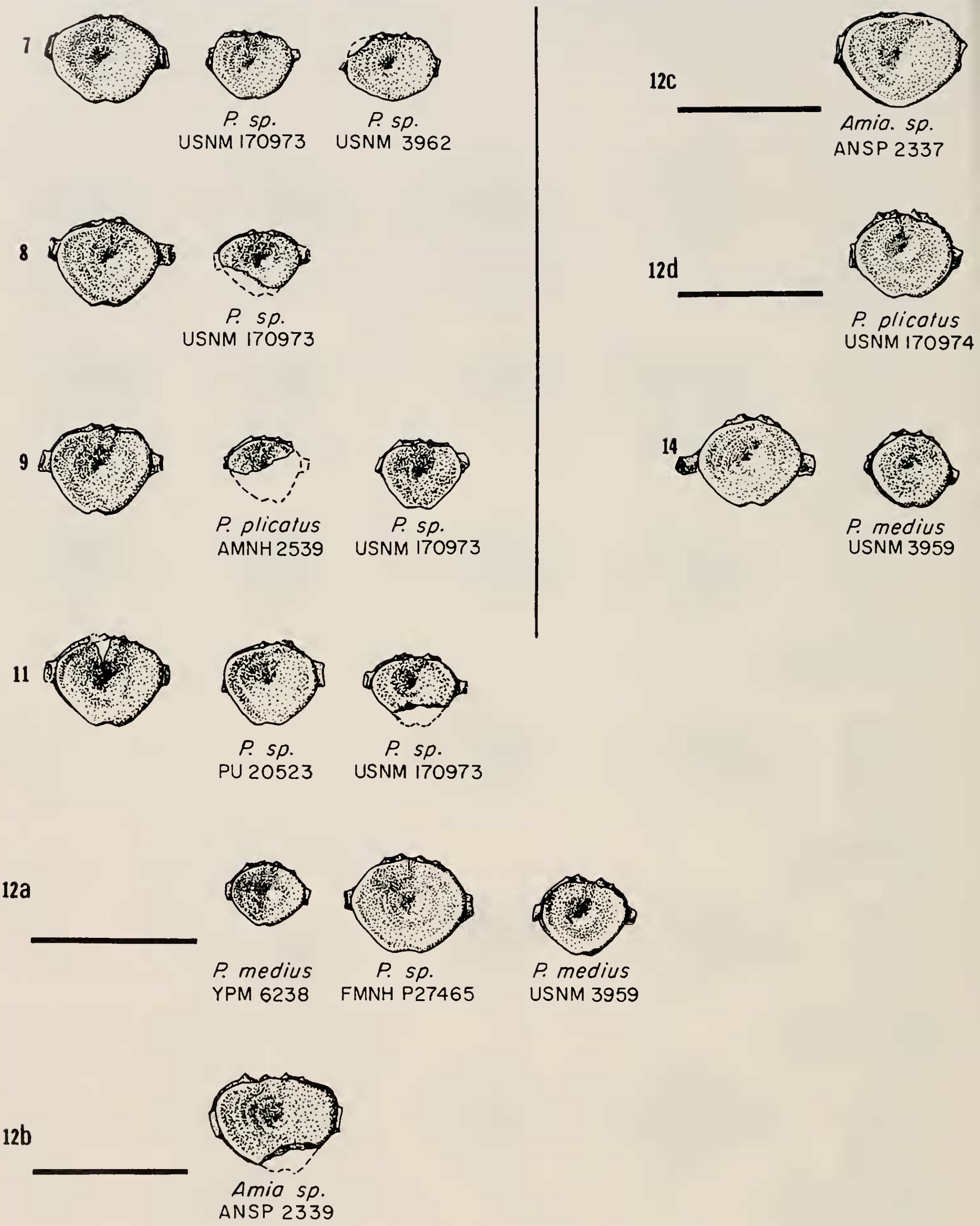


Fig. 23. Seventh through fourteenth mid-trunk vertebrae of *Amia uintaensis* compared with type specimens of synonymized taxa (refer to Table 15 for data).

however, differ meristically from that of *A. calva* and *A. scutata* in number of vertebrae in the various regions. There are 31 trunk centra in *A. uintaensis* (PU 13865), as opposed to 37 (mean) in *A. calva* and 36 (mean) in *A. scutata*. The number of diplospondylous vertebrae is 20–21, as compared with 14–17 in *A. calva* and 15 in *A. scutata*. This variation from *A. calva* and *A. scutata* in the organization of the verte-

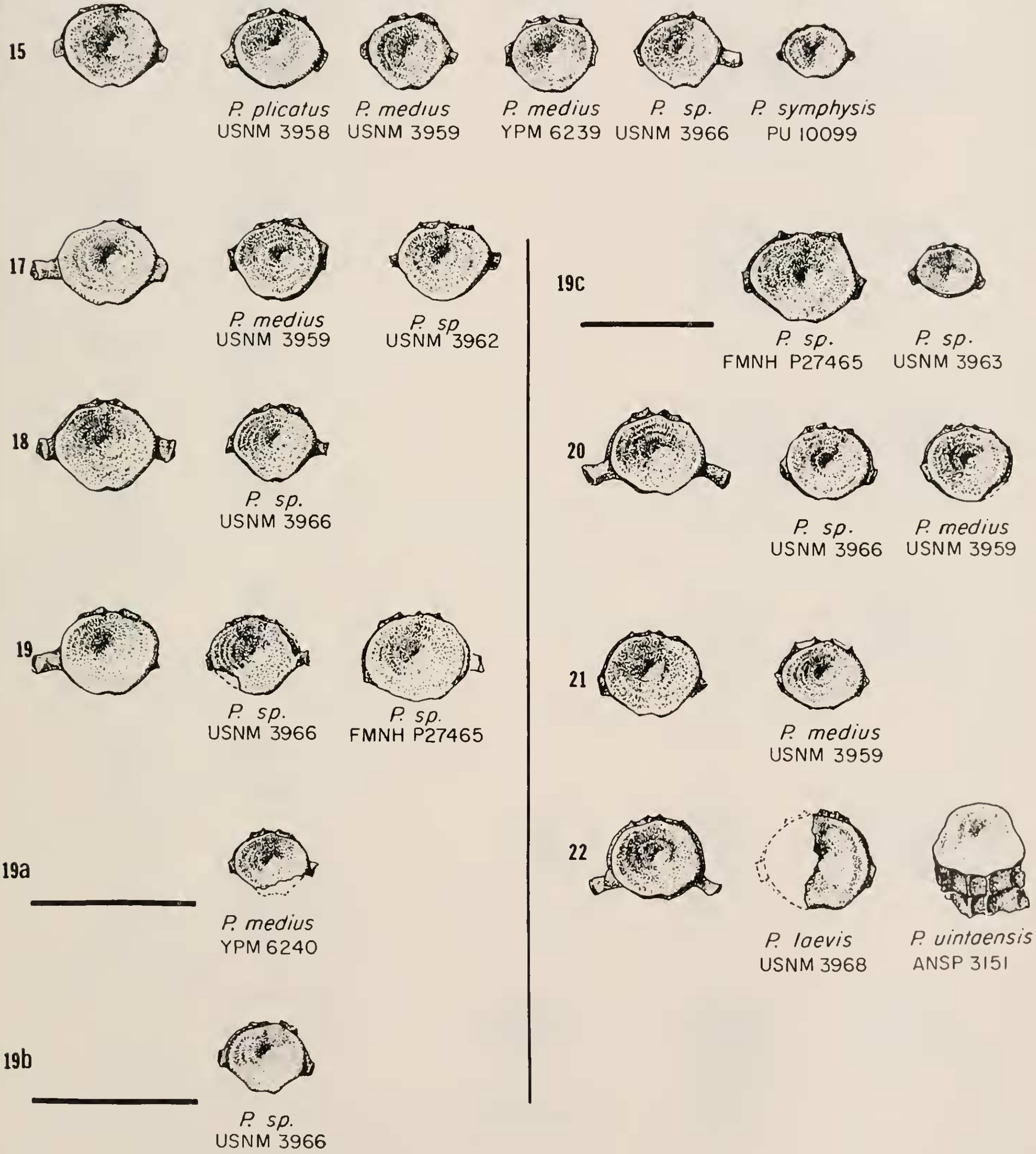


Fig. 24. Fifteenth through twenty-second posterior trunk vertebrae of *Amia uintaensis* compared with type specimens of synonymized taxa (refer to Table 16 for data).

Fig. 25. Posterior trunk and caudal vertebrae of *Amia uintaensis* compared with type specimens of synonymized taxa (refer to Table 17 for data).

TABLE 15. ANGLE OF BASAPOPHYSES, LENGTH, HEIGHT, AND WIDTH OF VERTEBRAE OF *Amia uintaensis* COMPARED WITH TYPE SPECIMENS OF SYNONYMIZED TAXA AS ILLUSTRATED IN FIGURE 23

Relative Vertebral Number	Specimen	Angle of Basapophyses (Degrees)	Length (mm)	Height (mm)	Width (mm)
7	*P. sp.* USNM 170973	179°	8.5	19.5	25.5
	P. sp. USNM 3962		7.0	20.0	28.0
8	*P. sp.* USNM 170973	178°	8.5	19.5*	26.0
9	*P. plicatus* AMNH 2539	177°	6.0*	18.0*	24.0
	P. sp. USNM 170973		8.0	21.0	25.5
11	*P. sp.* PU 20523	174°	7.5	25.0	30.0
	P. sp. USNM 170973		7.5	22.0*	25.0
12a	*P. medius* YPM 6238	171°	6.0	19.0	24.0
	P. sp. FMNH P27465		11.0	30.0	35.0
	P. medius USNM 3959		9.0	22.0	28.0
12b	*Amia sp.* ANSP 2339	167°	10.0	29.0*	40.0
12c	*Amia sp.* ANSP 2337	166°	10.0	29.0	38.5
12d	*P. plicatus* USNM 170974	163°	8.0	24.0	30.0
14	*P. medius* USNM 3959	160°	7.5	19.0	23.0

* Est.

TABLE 16. ANGLE OF BASAPOPHYSES, LENGTH, HEIGHT, AND WIDTH OF VERTEBRAE OF *Amia uintaensis* COMPARED WITH TYPE SPECIMENS OF SYNONYMIZED TAXA AS ILLUSTRATED IN FIGURE 24

Relative Vertebral Number	Specimen	Angle of Basapophyses (Degrees)	Length (mm)	Height (mm)	Width (mm)
15	*P. plicatus* USNM 3958	156°	8.5	22.5	25.0
	P. medius USNM 3959		8.5	23.0	27.0
	P. medius YPM 6239		8.5	22.0	24.5
	P. sp. USNM 3966		8.5	21.0	25.5
	P. symphysis PU 10099		5.5	15.5	20.0
17	*P. medius* USNM 3959	153°	9.0	24.0	29.0
	P. sp. USNM 3962		9.0	23.0	28.0
18	*P. sp.* USNM 3966	149°	9.0	21.0	25.5
19	*P. sp.* USNM 3966	143°	8.5	23.0	27.8
	P. sp. FMNH P27465		11.0	28.0	33.0
19a	*P. medius* YPM 6240	139°	7.0	19.0	23.0
19b	*P. sp.* USNM 3966	138°	—	—	—
19c	*P. sp.* FMNH P27465	136°	11.0	25.0	35.0
	P. sp. USNM 3963		7.0	16.5	20.0
20	*P. sp.* USNM 3966	132°	9.0	21.0	27.0
	P. medius USNM 3959		9.0	22.0	26.0
21	*P. medius* USNM 3959	122°	9.5	22.0	27.0
22	*P. laevis* USNM 3968	117°	10.0	26.0	30.0
	P. uintaensis ANSP 3151		12.0	28.0	29.0

Table 17. Angle of basapophyses, length, height, and width of vertebrae of *Amia uintaensis* compared with type specimens of synonymized taxa as illustrated in figure 25

Relative Vertebral Number	Specimen	Angle of Basapophyses (Degrees)	Length (mm)	Height (mm)	Width (mm)
24	*P. sp.* YPM 6242	102°	9.0	17.0	22.0
26	*P. uintaensis* ANSP 3151	97°	10.0	23.0	28.0
27	*P. laevis* PU 10109	90°	13.0	29.0	33.0
28	*P. laevis* PU 10109	83°	14.0	28.0	30.0
29	*P. media* ANSP 5632	80°	8.0	16.0	18.0
30	*P. sp.* USNM 3963	62°	11.0	—	—
	P. symphysis PU 10110		6.0	14.0	13.5
31	*Amia sp.* ANSP 2338	46°	13.0	26.0	23.0
	A. macrospondyla NMC 6198		12.0	25.0	22.0
34	*P. laevis* USNM 3968		6.5	22.0	18.0
39	*P. sp.* FMNH PF 4509		7.0	19.0	18.0
43	*P. sp.* USNM 3966		7.0	19.0	18.0
44	*P. medius* USNM 3959		6.0	16.0	18.0
45	*P. medius* USNM 3959		5.5	17.5	18.0
50	*P. sp.* USNM 5450		7.0	15.0	13.5
51	*P. medius* USNM 3959		5.0	17.0	11.0
59	*P. corsonii* USNM 3961		4.0	11.0	10.0

bral column into regions and types of vertebrae appears to be a useful taxonomic character of *A. uintaensis.*

The neural, aortal, and haemal facets do not appear to vary much from those of *A. calva.* The first six ventral aortal facets show basically the same pattern for both species (Figs. 11, 22). The angle of basapophyses in *A. uintaensis* differs from that of *A. calva* in two ways. The first six vertebrae all have basapophyseal angles of 180 degrees, and it is not until the seventh vertebra that these angles gradually begin to decrease. Because of this more posterior beginning in the decrease of the angles and because there are fewer trunk vertebrae, the rate of decrease of the basapophyseal angle is greater. These angles range from 180 degrees anteriorly to approximately 45 degrees posteriorly, about the same as the range for *A. calva.*

The intracolumnar variation in centrum shape seen in the vertebral column of Recent *A. calva* also occurs in *A. uintaensis* (Fig. 14). In some respects the latter shares certain characteristics with *A. calva.* The first centrum is broad and thin, and usually lacks basapophyses (Fig. 22). However, centra between the fourth and twentieth vertebrae begin to acquire an almost subtriangular outline, as opposed to the subelliptical form of the *A. calva* trunk centra (Fig. 12). The subtriangular shape may be a function of greater size of the centra.

The chordal foramen is open in all known vertebrae of *A. uintaensis* from the Paleocene, Eocene, and Oligocene, but is often filled with detritus during fossilization. Estes (1964: 42) observed that Cretaceous specimens as well as the Late Paleocene specimen (PU 16236) had the chordal foramen smoothly closed with bone. A re-examination of PU 16236 reveals that the chordal foramen is actually filled with fine sediment rather than bone, so that the character of the closed foramen can only be applied to the Cretaceous specimens. Chordal foramen position in all specimens shows slight intracolumnar variation along the trunk as in *A. calva*, although occurring more dorsally. In the caudal region there is virtually no difference between the two forms.

Leidy characterized *"Protamia" uintaensis* on the basis of five centra and one basioccipital. His height/width proportions were described in relation to those in an undiagnostic intracolumnar standardization of the centra of the *A. calva* vertebral column. My measurements of the anterior trunk centra reveal that the holotype ANSP 5558 has a width 1.3 times the height, and paratype ANSP 8044 has a width 1.6 times the height. Other paratype centra are posterior trunk centra with width/height ratios of approximately 1:1. Romer and Fryxell (1928: 521) described a displaced posterior trunk centrum as having a height of 10 mm and a width of 12.5 mm, about the same as in ANSP 5558. Estes (1964: 43), in his discussion of the height/width proportions of *A. uintaensis* centra, misinterpreted Leidy's (1873a, 1873b) diagnosis of *"Protamia" uintaensis* and Romer and Fryxell's (1928) diagnosis of *"Paramiatus gurleyi,"* indicating that vertebrae of the former were three times as wide as deep, those of the latter two times. Estes was correct, however, in his assumption that there is intracolumnar variation in height/width ratios.

The general pattern of intracolumnar variation in the *A. uintaensis* vertebral column is quite similar to that of *A. calva;* there is the same trend from horizontally elliptical centra to circular or vertically elliptical centra (Fig. 14). Thus the earlier diagnoses of *A. uintaensis* using height/width ratios that attributed the proportions of the anteriormost trunk vertebrae to the entire column are undiagnostic.

On the basis of isolated centra and skull material, the most commonly used character in differentiating *A. uintaensis* from *A. calva* has been the former's greater size. However, the articulated specimen (PU 13865), which is the smallest known *A. uintaensis,* is only 146 mm longer than *A. fragosa* (FMNH 2201) and 16 mm longer than the largest *A. calva* known to me (UMMZ 197683). Estes (1964) suggested that the widening of the *A. uintaensis* vertebrae might be a function of its greater size; Gould's (1966) statement that internal elements generally increase at allometric rates to provide sufficient surface area to maintain the external surface area offers a partial explanation as to why the large *A. uintaensis* vertebrae have greater width in proportion to height than they do in smaller amiid vertebrae.

Discussion

Two species of *Protamia,* one species of *Hypamia,* six species of *Pappichthys,* and three species of *Amia* have been described on vertebral characters from isolated centra and disarticulated cranial elements (Table 19). With the exception of *Amia whiteavesiana, A. selwyniana,* and *A. macrospondyla* from the Oligocene Cypress Hills Formation of Alberta, all these taxa are based on material from the Bridger Basin, Bridger Formation, of Wyoming. Each of these 12 taxa will be re-evaluated in the following discussion. Of the twelve species and four genera, *"Protamia" uintaensis* (Leidy, 1873a) is the oldest name. Leidy's type specimens are all trunk vertebrae. The holotype ANSP 5558 (Fig. 22) is approximately the sixth anterior vertebra and displays the characteristic subtriangular outline of other specimens. The paratypes include trunk vertebrae (ANSP 8044, 3151), and a large basioccipital (ANSP 5622). The holotype vertebrae and the basioccipital are considered diagnostic for *Amia uintaensis,* on the basis of their possessing the characteristic subtriangular vertebral outline, and a kidney-shaped articular surface of the basioccipital.

Leidy (1873a) described *Protamia media* from two large trunk centra from the

Bridger Formation of Wyoming. His main criterion for distinguishing this form from *A. calva* and from the other species of "*Protamia*" was that the vertebrae were twice the size of *A. calva* vertebrae and "somewhat smaller than *Protamia uintaensis*" (Leidy, 1873b). The holotype USNM 2181 appears to be from the anterior trunk region (approximately the seventh or eighth centrum, as suggested by its proportions and configurations of aortal facets). The basapophyseal angle is approximately 178–180 degrees. The paratype ANSP 5632 is from the posterior trunk region, with an 80-degree basapophyseal angle, which is approximately equivalent to the twenty-ninth centrum in *A. uintaensis* (Table 17; Fig. 25). Cope (1884, plate 4, figs. 7–20) figured "*Pappichthys medius*" on the basis of 14 disarticulated centra from the same locality (USNM 3959). Eight of these are from the trunk region and correspond to centra within the anterior to mid-trunk region of *A. uintaensis* (Tables 15–16; Figs. 23–24). The remaining six centra correspond to centra in the caudal region (Tables 16–17; Figs. 24–25). Cope gave no description, but in figuring these specimens he allocated to them his own genus, emending Leidy's (1873a) prior nomenclature. Both Leidy and Cope had apparently assumed that the characteristics of one or a few vertebrae represented those of the entire column. Both species fall well within the size range of *A. uintaensis* (Tables 14–17), and are here considered synonyms of the latter.

Leidy (1873a) described *Hypamia elegans* from one small trunk vertebra. He characterized this form as possessing a centrum that was characteristically "short in proportion with its breadth, and it presents sutural impressions for a contiguous pair of neural arches" (Leidy, 1873b). ANSP 5580 appears to be from the mid-trunk region, comparable to approximately the nineteenth centrum as suggested by its proportions and configuration of aortal facets. The basapophyseal angle is 138–139 degrees. These character-states and the small size are not unique, occurring as the do in all the other species of *Amia; Hypamia elegans* is therefore a *nomen dubium.*

Cope (1873) described *Pappichthys plicatus* from the anterior portion of a large left dentary (AMNH 2539). Other type material included two premaxillae, a right quadrate, a left epihyal, an anterior portion of an ectopterygoid, three trunk vertebrae, and numerous fragments of angulars. He characterized this form primarily on the basis of dermal sculpture of the "cranial fragments being roughly grooved." The angular in *A. uintaensis* is generally marked by more pronounced dermal sculpture than the other mandible elements. His diagnosis of the vertebrae (USNM 3958) is based on proportions and morphology of neural and aortal facets, both of which correspond to various trunk vertebrae in *A. uintaensis* (Tables 15–16; Figs. 23–24). The description of the remaining elements conforms with other elements of *A. uintaensis. Pappichthys plicatus* is therefore a synonym of the latter.

Cope (1873) described *Pappichthys sclerops* from a large left dentary. He characterized this form as possessing a dentary "more compressed and deeper" than that in *A. calva* and other species of "*Pappichthys.*" The dentary (USNM 3965) in all respects greatly resembles all dentaries that have been referred to *A. uintaensis,* and I regard *Pappichthys sclerops* as a synonym of the latter.

Cope (1873) described *Pappichthys laevis* from a large anterior dentary fragment (USNM 3968). Other type materials include a premaxillary fragment, fragments of angulars (AMNH 2570), a left quadrate fragment, a trunk vertebra fragment, and a caudal vertebra. Although Cope distinguished this taxon from other species of *Pappichthys* on vertebral proportions, variances in dermal sculpture, dentary alveolar count, and obliqueness of alveolar face, these character-states occur in *A. uintaensis. Pappichthys laevis* is therefore a synonym of the latter.

Cope (1873) described *Pappichthys symphysis* from two large fragments of trunk vertebrae and a ural (USNM 3960). His diagnosis rests primarily on configuration of neural facets and basapophyseal length. Osborn *et al.* (1878: 104) later reported two caudal vertebrae as cotypes (PU 10099, 10110). Cope (1873) described *Pappichthys corsonii* from 12 centra (USNM 5475–5476), a basioccipital (USNM 5476), and a left dentary fragment (USNM 3961). He distinguished this form from *Pappichthys symphysis* on different neural facet morphology, basapophyseal length, and height/width proportions. Merrill (1907: 14) cites "*Pappichthys symphysis* = *Pappichthys corsonii*" without further discussion. The centra of both forms conform to centra in the vertebral column of *A. uintaensis* (Table 17; Fig. 25) and the characters assigned to the dentary and basioccipital of *Pappichthys corsonii* are also found in *A. uintaensis;* thus both *P. symphysis* and *P. corsonii* are synonyms of *A. uintaensis.*

From the Early Oligocene Cypress Hills Formation, Saskatchewan, Cope (1891) described *Amia whiteavesiana* from an anterior vertebra (NMC 6197), and *Amia macrospondyla* from a caudal vertebra (NMC 6198). Both these forms were founded on variations of vertebral characters (height/width proportions, lack of basapophyses, and chordal foramen position) that are also represented in the vertebral column of *A. uintaensis.* The type centrum of *A. whiteavesiana* corresponds approximately to the second anterior vertebra in *A. uintaensis* (Table 14; Fig. 22), that of the type centrum of *A. macrospondyla* with the thirty-first centrum in *A. uintaensis* (Table 17; Fig. 25). Prior to the appearance of Cope's (1891) publication, Ami (1891), in his review of the Cypress Hill fauna, mistakenly listed *A. whiteavesiana* under the name *A. selwyniana. A. macrospondyla* and *A. whiteavesiana* are here considered synonyms of *A. uintaensis; A. selwyniana* is a *nomen nudum.*

Comments on European and Asian Forms

Janot (1967) described a large amiid, *Amia robusta,* from the Late Paleocene of France, on the basis of disarticulated material. She distinguished this form from *A. calva* and *A. russelli* on the angle of the ventral border of the dentary face, and on morphology of the parasphenoid tooth-bearing surface in addition to other minor morphological differences. Many of the diagnostic elements or associations on which *A. uintaensis* is based, such as coronoid and vomerine teeth, regional vertebral counts and dorsal cranial elements, are missing in her material. The elements that she does figure, however, closely resemble the comparative bones in *A. uintaensis.* Similarities include rounded distal ends of branchiostegal rays (also in *A. fragosa*), subtriangular morphology of trunk vertebrae, extensive surface of parasphenoid tooth-patch, and shallow orbital notch in frontal (also in *A. scutata* and *A. calva*). These marked similarities suggest that *A. robusta* is a synonym of *A. uintaensis.* Current work on the relationship of the North American and European continents in the Early Cenozoic (McKenna, 1972) indicates that they were connected until the Early Eocene and that there is great similarity between the Paleocene and Early Eocene mammalian taxa at that time. There is thus no zoogeographic problem inherent in synonymizing these two species.

Hussakof (1932) described *Pappichthys mongoliensis* from disarticulated elements from the Late Eocene Ulan Shireh beds of the Shara Murun region, Inner Mongolia (collected by the American Museum Central Asiatic Expeditions.) At the time of Hussakof's description, this collection (AMNH 6372) represented the most extensive material of "*Pappichthys.*" The collection includes numerous dentaries, maxillae, three gulars, three opercula, three cleithra, an hyomandibular, a supracleithrum, a vomer, and trunk and caudal vertebrae.

Hussakof distinguished this form from *A. calva* by the length of the dentaries and the morphology of the operculum, and from species of *"Pappichthys"* and *"Protamia"* on the basis of comparison of vertebral size. A comparison of the Mongolian material with *A. uintaensis* shows some dissimilarities, but there is still a closer affinity between this form and *A. uintaensis* than with the other species of *Amia.* The vomer bears numerous sharp vomerine teeth; the hyomandibular is deeply arched, and the lingual face of the dentaries conforms to that of *A. uintaensis.* The dentary, however, is quite elongated anteriorly, the supracleithrum is narrower, and the dorsal border of the operculum is short and ascends at a 30-degree angle rather than being horizontal as in *A. uintaensis* (and in other *Amia* species). The extrascapular is narrow and tapered to a point rather than flattened medially. Thus, although *Pappichthys mongoliensis* is similar to *A. uintaensis* in many features and is clearly related to it, it also differs in some respects. It undoubtedly belongs to the genus *Amia,* and retention of all the Mongolian specimens in *Amia mongoliensis* seems the most practical alternative at this time. The Mongolian higher vertebrate taxa indicate that the Turgai Straits at least partially isolated Mongolia from Europe during at least part of the Cretaceous, Paleocene, and Eocene, and that probably little exchange took place until the Late Eocene (Szalay and McKenna, 1971: 280–281). It may be possible that *A. mongoliensis* evolved from *A. uintaensis* during this migration.

Amia cf. *uintaensis*

Hypodigm. CRETACEOUS. Lance Formation, Wyoming: CM 256, YPM 6311, trunk vertebrae; UCMP 56276, two fragments of a single vertebra; UCMP 56277, one complete vertebra, one vertebral fragment, one left maxillary fragment. Hell Creek Formation, Montana: AMNH 6385, trunk vertebra; MCZ 9334, dentary tooth tips. Aguja Formation, Texas: UMM collections, maxillary fragment. Ojo Alamo Formation, New Mexico: USNM collections, trunk vertebra.

Discussion

Cretaceous specimens of large amiids occur in both Lance and Hell Creek formations and consist mostly of isolated and broken centra, and teeth that have been identified primarily on the basis of size. The characteristic subtriangular outline of the trunk vertebrae is even more pronounced in these Cretaceous specimens, wherein the lateral centrum walls between the basapophyses and the aortal facets are concave (Fig. 26). The chordal foramen is, as Estes (1964: 42) noted, closed with bone, as are one-third of the vertebrae referred to *A. fragosa* from the Lance Formation. However, Estes observed lateral concavities between the neural facets and basapophyses in a large vertebral centrum (AMNH 6385) from the Hell Creek Formation (mistakenly cited by him as AMNH 6835 from the Oldman Formation of Alberta). Estes apparently confused neural with aortal facets and thus figured the vertebra upside down. Correct orientation of the centrum (Fig. 26) shows concavities between the basapophyses and the aortal facets. Thus, Estes was incorrect in concluding that *A. fragosa, A. calva,* and the Eocene specimens of *A. uintaensis* "also seem to lack the concavity between the 'basapophysis' and neural arch present in the large Cretaceous specimens." Two other specimens from the Lance Formation (YPM 6311, CM 256; Fig. 26) also show the prominent concavities between the basapophyses and aortal, rather than neural, facets. In addition to the vertebrae, Estes described a maxillary fragment as being larger and more robust than that of *A. fragosa,* although "characteristically amiid in tooth implantation and general shape." A more complete maxillary fragment (UMM collections) from the Aguja Formation (Big Bend National Park, Brewster County, Texas) conforms with Estes' (1964) description.

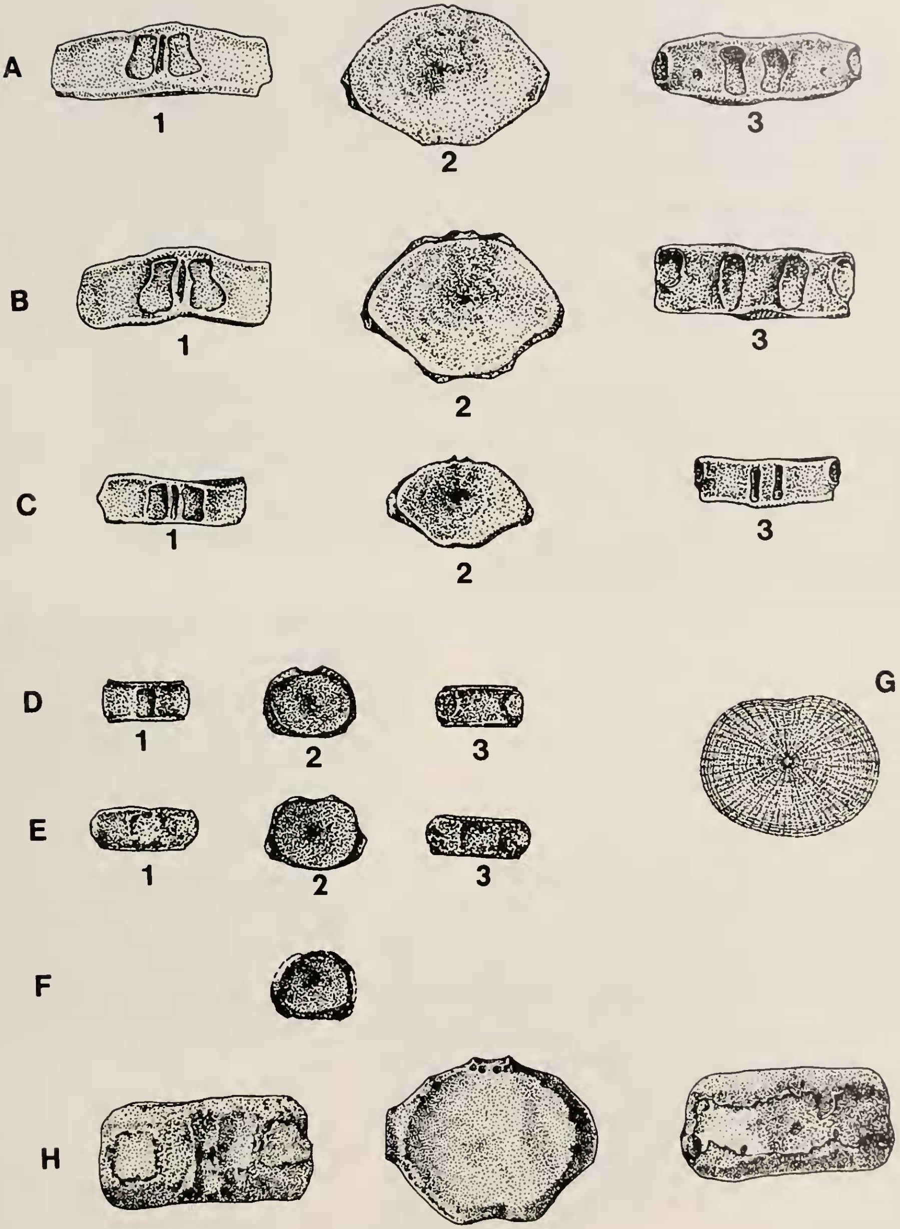


Fig. 26. Comparison of different Cretaceous vertebrae. *Amia* cf. *uintaensis:* A, anterior trunk vertebra, CM 256, Lance Formation, Wyoming; B, posterior trunk vertebra, AMNH 6385, Hell Creek Formation, Montana; C, mid-trunk vertebra, YPM 6311, Lance Formation, Wyoming. Chondrichthyes: D, E, G (thin section), trunk vertebrae, FHKSCM 13024–9, Black Creek Formation, North Carolina; F, trunk vertebra, MCZ 12879, Peedee Formation, North Carolina. Cetacean: H, caudal vertebra, FHKSCM 13025, Calvert Formation?, North Carolina.
1 = dorsal, 2 = articular surface, 3 = ventral

Only three new centra and a maxillary fragment have been identified since Estes' (1964) study. The vertebrae, as noted above, differ in certain minor respects from the Paleocene and Eocene specimens. Whether or not this material actually represents *A. uintaensis* or an earlier stage of evolution can only be determined when more complete Cretaceous material is available.

Amia scutata Cope, 1875

Amia dictycephala Cope, 1875: 3.
Amia exilis Lambe, 1908: 12.

Holotype. USNM 5374, incomplete specimen lacking the head and body anterior to the middle of the dorsal fin; anal and part of dorsal and caudal fins well preserved.

Type locality and horizon. Florissant, Colorado. East half of section 2, T 13 S, R 71 W, Teller County, Colorado; Florrisant Formation.

Age Range. Chadronian (Early Oligocene) to Orellan (Middle Oligocene).

Hypodigm. OLIGOCENE. Cypress Hills Formation, Saskatchewan: NMC 6200, 6205, vertebrae; NMC 6201, basioccipital. Chadron Formation, South Dakota: PU 17172, left dentary with posterior coronoid bearing teeth, and a trunk vertebra. Lower Brule Formation, South Dakota and Nebraska: FMNH PF4508, PF4509, CM 3814, vertebrae; FMNH PF4506, right vomer bearing teeth. Florissant Formation, Colorado: PU 10172, nearly complete specimen (counterpart = YPM 6243, anterior half; USNM 4087, caudal half); YPM 6241, complete caudal region (with counterpart); UMMP V-57431, nearly complete specimen; USNM 3992, partial specimen, lacking skull and tail; AMNH 2802, nearly complete skull; AMNH 2670, partial specimen, lacking skull and caudal region; AMNH 2671, caudal region.

Known distribution. South Dakota, Nebraska, Colorado, and Saskatchewan.

Revised diagnosis. Vertebral meristics similar to those of *A. calva,* but head/standard-length proportion is intermediate between that of *A. uintaensis* and *A. calva.* Extrascapular thicker at distal end than in *A. calva,* with concave posterior border. Pterotic more similar to that of *A. uintaensis* than of *A. calva;* anterior portion narrow and extended laterally to the frontal. Orbital excavations more marked than in *A. calva,* but not as deep as in *A. uintaensis* or *A. fragosa.* Preoperculum resembles that of *A. uintaensis* more than that of *A. calva,* being narrower dorsally than ventrally. Symphyseal incurving of the dentary less than in *A. calva,* but greater than in *A. uintaensis.* Ventroposterior process of cleithrum heavily sculptured as in *A. fragosa* and *A. uintaensis.* Infraorbital 4 larger than infraorbital 5 as in *A. fragosa* and *A. uintaensis.* Ossification of cranial bones extensive as in other fossil species, greater than in *A. calva.* Greatest known standard-length 390 mm.

Introduction

Cope's (1875: 3) description of *Amia scutata* is based on a specimen lacking the head and body anterior to the middle of the dorsal fin, from the Middle Oligocene Florissant Formation near Florissant, Colorado. He distinguished this form from *Amia dictyocephala* (found in the same deposit; Cope, 1875) and *Amia calva* by its larger scales "of which only seven and a half longitudinal rows are visible above the vertebral column." Cope described *A. dictyocephala* from two partially complete specimens lacking skulls and caudal fins (USNM 3992, AMNH 2670), two complete caudal regions (AMNH 2671, USNM 4087), and a nearly complete skull (AMNH 2802); Osborn *et al.* (1878) later described another specimen of *A. scutata* from the same deposit. This specimen was more complete, consisting of an axial skeleton and a crushed skull. They believed *A. scutata* to be a valid form, differing from *A. calva* in having a proportionately larger head.

Comparison of known specimens of *A. scutata* revealed that the counterparts to the specimen described by Osborn *et al.* (PU 10172) were separated and sold to two

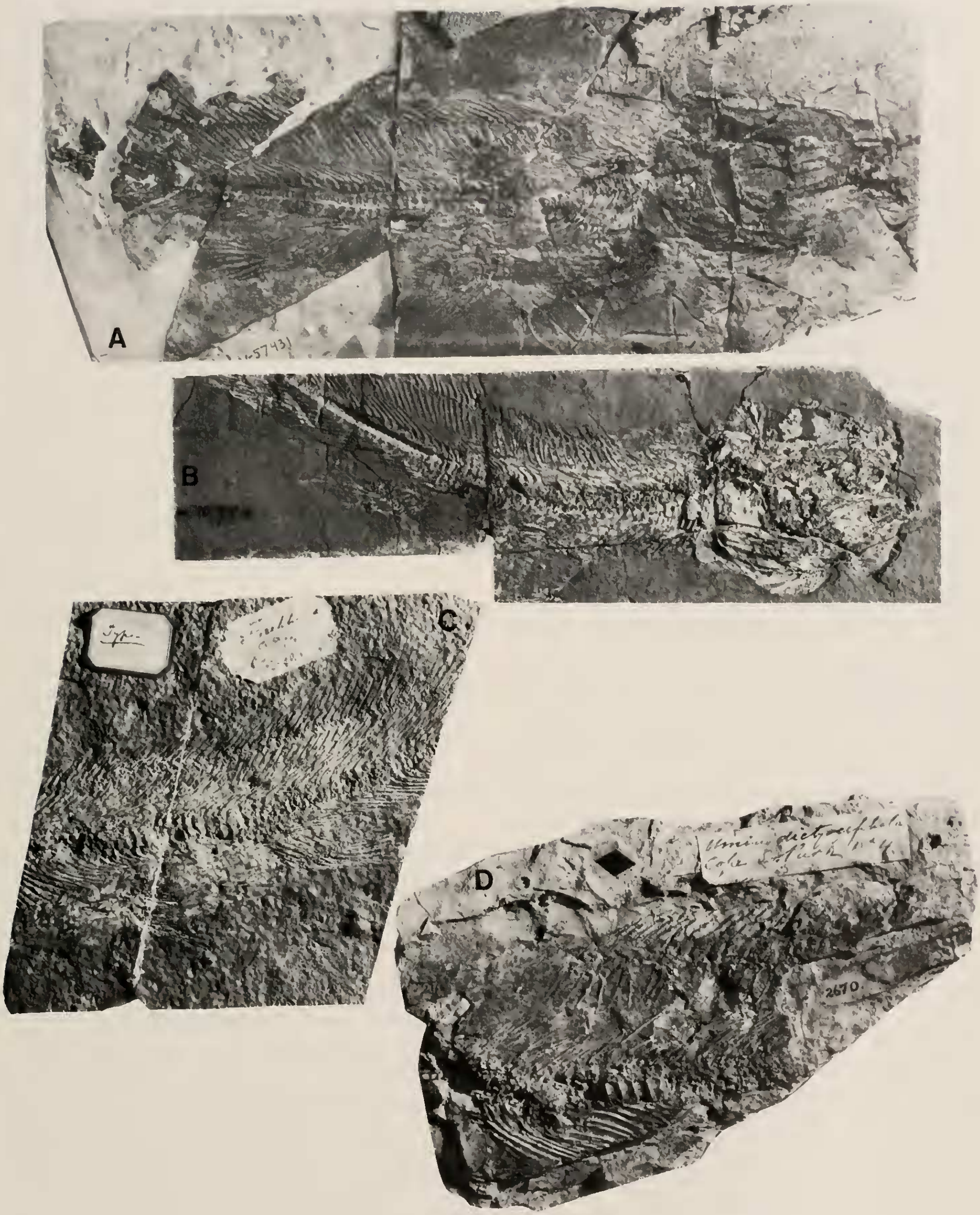


Fig. 27. A, *Amia scutata* UMMP V-57431; B, *A. scutata* PU 10172; C, *A. "dictyocephala"* USNM 3392; D, *A. "dictyocephala"* AMNH 2670.

different museums. The caudal portion of the counterpart was found in the National Museum of Natural History (USNM 4087) and is one of the paratypes used by Cope (1875) in his description of *A. dictyocephala.* The anterior region was found unlabeled at the Yale Peabody Museum (YPM 6243; Plate 4).[1]

In 1967 another nearly complete specimen was discovered from the same deposit (Fig. 27A) and Cavender (1970: 42) reported the specimen *A. dictyocephala* as differing from *A. calva* in having a larger infraorbital 4, in the sculpture of cleithrum, and "by its proportionately larger head and orbit, and somewhat shorter body."

Fossil Record

Other than the Florissant Formation, the only deposits from which elements of *A. scutata* can be identified are the Cypress Hills Formation of Saskatchewan, Chadron Formation of South Dakota, and the Lower Brule Formation of South Dakota and Nebraska. Becker (1961: 38) reported amiid scales (UMMP collections) from the Late Oligocene Passamari Formation and Middle Oligocene Grant Horse Prairie Shale of Montana (Becker, 1962). Since no specific characters for scales of *Amia* have yet been determined, it is best to allocate this material to *Amia* sp. Skinner *et al.* (1968: 415) has reported *Amia* sp. vertebrae (F:AM 42947) from the Early Miocene Turtle Butte Formation of South Dakota. Only two specimens were found; since the vertebrae of *A. scutata* and *A. calva* are morphologically and meristically similar, Skinner *et al.'s* identification is the only possible one at this time. The stratigraphic range of *A. scutata* is therefore limited to the Early and Middle Oligocene.

Description

Neurocranium. The basioccipital (PU 10172, NMC 6201) is similar to that of *A. calva.* The only available parasphenoid (PU 10172) is poorly preserved, but closely resembles that of *A. calva* in length and position of ascending processes.

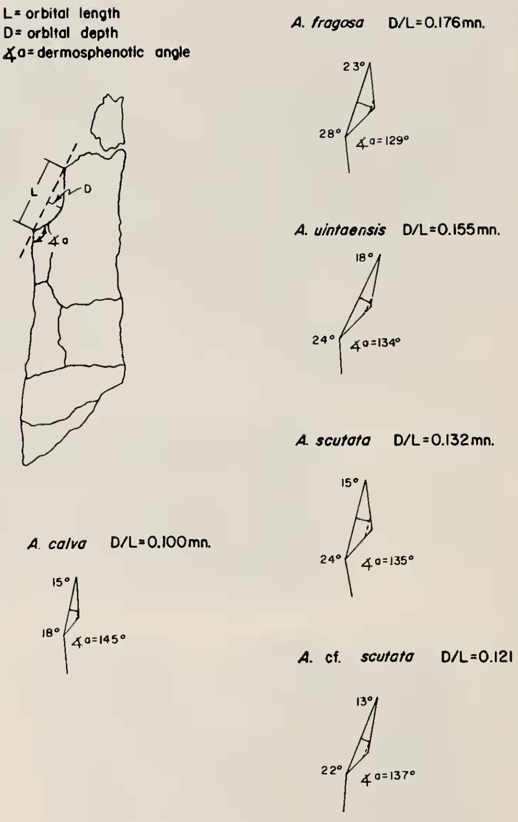


Fig. 28. Orbital dimensions of *Amia* spp.

The extrascapular in *A. scutata* differs slightly from that of *A. calva* in that the distal end is relatively thicker and the posterior lappet is less pronounced; also, the posterior border is more convex (Fig. 15). As in *A. calva,* however, the proximal anterior corner is squared off, and the medial suture is relatively long. The pterotic in *A. scutata* resembles that of *A. uintaensis* more than that of *A. calva* in general morphology, since the anterior half is narrower than the posterior half; in the Recent species the ends are nearly symmetrical. The anterior border extends further laterally than in *A. calva,* and, as in *A. uintaensis,* adjoins the distal lateral side of the frontal, rather than the posterior border as in *A. calva.* The dermosphenotic, parietal, frontal, and nasal of *A. scutata* conform to these bones in *A. calva.* The parietal/frontal ratio is marginally within the lower limit of the range of *A. calva* (Table 7). The orbital excavation in the

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[1] The counterparts (USNM 4087, YPM 6243) to PU 10172 have been subsequently acquired by the Museum of Natural History, Princeton University.

frontal (Fig. 28) is greater than in *A. calva* but less than in *A. fragosa* or *A. uintaensis.* Suprascapulars, antorbitals, and rostrals are not preserved.

The lacrimal is similar to that of *A. calva,* bearing a posterior notch for the reception of infraorbital 2, but in *A. scutata* the lacrimal is more robust. Infraorbital 2 and infraorbital 3 are similar to these bones in *A. calva.* Infraorbital 4 is more massive posteriorly than in *A. calva;* it exceeds infraorbital 5 in dorsoventral length, and the posterodorsal corner, which in *A. calva* is markedly acute is, in *A. scutata,* more squared off. This bone more closely resembles that of *A. fragosa;* it is not available for comparison in *A. uintaensis.* Infraorbital 5 is less massive posteriorly than in *A. calva;* in this feature it resembles that of *A. fragosa.* It is also, as in *A. fragosa* and *A. uintaensis,* deeper anteriorly than in *A. calva.*

Branchiocranium. The supramaxilla in *A. scutata* is elongated and tapered to a point anteriorly, with a relatively straight ventral border as in *A. calva.* It is slightly longer and more robust posteriorly, the posterodorsal border being higher and less obliquely curved than in *A. calva, A. uintaensis,* and *A. fragosa.* The premaxilla resembles that of *A. calva.* The maxilla is wider posteriorly and more ossified anteriorly than that of *A. calva,* but otherwise agrees with the bone in the Recent species.

Dermopalatine, autopalatine, entopterygoid, ectopterygoid, metapterygoid, and vomer are not preserved. However, conical vomerine teeth are displayed on PU 10172, and resemble those of *A. calva* rather than those of *A. fragosa* or *A. uintaensis.* The relative number of teeth and their extent on the vomer cannot be discerned.

As in *A. calva* and *A. uintaensis,* the dentary in *A. scutata* lacks the dorsal shelf adjacent to the lingual border of the alveolar ridge seen in *A. fragosa* (Fig. 18). The bone is very thick, especially toward the mid-lingual surface, where the dorsal and ventral halves meet to form the Meckelian groove. As in *A. uintaensis* the upper wall of this groove is primarily formed by the thickness of bone in dorsal half of the lingual surface; the ventral half is barely overlain by the dorsal half. The first coronoid does not extend past the Meckelian groove, and bears sharp conical teeth, as in *A. calva* (Fig. 18). The anterior half of the dentary is more incurved than in *A. uintaensis,* but not to the extent that it is in *A. calva.* The anterior width of the dentary also resembles that of *A. calva* and *A. uintaensis* in that it is evenly tapered almost to the symphyseal edge. The angular and surangular are similar to comparable bones in *A. calva,* except that they, like the dentary, are more extensively ossified. The mandible/head-length ratio in *A. scutata* is well within this ratio range for *A. calva* (Table 7). The prearticular is not preserved.

The preoperculum is similar to that of *A. uintaensis,* being narrower dorsally than ventrally, rather than having both halves relatively equal in width, as in *A. calva.* The operculum resembles that of *A. calva* in morphology and operculum-depth/operculum-length (Table 7). The suboperculum and interoperculum resemble those of *A. calva* in general morphology, but the suture between them is longer anteroposteriorly. The branchiostegal rays are squared off distally, as in *A. calva.*

Post-cranial skeleton. The supracleithrum and metacleithrum are not preserved. The only part of the cleithrum available for study is the ventroposterior process in UMMP V-57431 which in *A. calva* is the only area of this bone that is visible externally. This region of the cleithrum in *A. scutata* is heavily sculptured (Fig. 21), and as in *A. uintaensis* and *A. fragosa,* this dermal ornamentation extends to the edge of the bone. In *A. calva,* this dermal structure is limited to the center and dorsal region of this part of the cleithrum.

The vertebral column of *A. scutata* resembles that of *A. calva* both in number of centra (Table 9) and in general morphology of the centra. The head/standard-length proportion (0.312) is greater than in *A. calva* (0.271), but less than in *A. uintaen-*

sis (0.322). The insertion of pectoral fin/standard-length and insertion of anal fin/standard-length ratios are both within the ranges of *A. calva*, although the latter proportion for *A. scutata* is somewhat greater than the mean for *A. calva* (Fig. 31).

Discussion

In the same paper as his description of *Amia scutata,* Cope (1875: 3) described *Amia dictyocephala,* also from the Florissant Formation. *A. dictyocephala* was distinguished from *A. scutata* by having 10 to 12 supravertebral scale rows, and 35 vertebrae between the anterior dorsal fin pterygiophore and the posterior anal fin pterygiophore (USNM 3992 AMNH 2670). He further characterized this form from a skull (AMNH 2802) that "possesses twelve branchiostegal rays, and a relatively smaller orbit than in *Amia calva.*" A re-examination of these specimens in the previous section on meristics showed that Cope's supravertebral scale row count was in error, and there is no perceptible difference in this feature between Recent and fossil *Amia* species (Table 8). In *A. calva,* the range for the number of centra between the insertion of the dorsal fin and the terminus of the base of the anal fin is 33–37. In the type specimen of *A. dictyocephala* (USNM 3992) the number of centra is 35, and the mean number in specimens of *A. scutata* is 36; there is clearly no way that this feature can be used to distinguish *A. dictyocephala* from *A. scutata* and *A. calva.* Cope, on the basis of AMNH 2802, thought that an orbit in *A. dictyocephala* was smaller than one in *A. calva,* but the small size was due largely to the constriction of the orbit that resulted from crushing of the dermosphenotic and upward displacement of infraorbital 5. The characters that Cope used to differentiate *A. dictyocephala* from *A. scutata* are undiagnostic, and my studies of the specimens show no morphological or meristic difference; *A. dictyocephala* is here considered to be a synonym of *A. scutata.*

Lambe (1908: 12–13) described *Amia exilis* from a single basioccipital (NMC 6201) and two mid-trunk vertebrae (NMC 6200, 6205) from the Early Oligocene Cypress Hills Formation of Saskatchewan. The temporal occurrence of these elements is equivalent to that of *A. scutata.* Lambe's description of the basioccipital conforms to that of *A. scutata* in being more extensively ossified than in *A. calva.* His diagnosis of the two centra is founded on height/width proportions, chordal foramen position, basapophyseal angle, and configuration of neural facets. Because *A. scutata* resembles *A. calva* in vertebral morphology, the characters that Lambe uses to distinguish *A. exilis* are undiagnostic; I therefore consider *A. exilis* as a synonym of *A. scutata.*

Amia cf. *scutata*

Hypodigm. MIOCENE. Pawnee Creek Formation, Colorado: UCMP 38222, nearly complete cranial roof, infraorbitals 4 and 5, nearly complete anterior portion of palate, two branchiostegal rays, maxillae, and right dentary.

Description

The general morphology of the cranial roof resembles both *A. scutata* and *A. calva* in parietal/frontal ratio (Table 7), rectangular parietals, and shape of dermosphenotic and nasal (Fig. 29). The extrascapular more closely resembles that of *A. scutata* in its greater width and less pronounced distal posterior lappets. The pterotic also resembles that in *A. scutata* in its being narrower anteriorly than posteriorly, and in bordering the frontal laterally rather than posteriorly. The size and depth of the orbital excavation is intermediate between that of *A. scutata* and *A. calva* (Fig. 28). The maxilla is similar to that of *A. calva,* being less robust posteriorly than that of *A. scutata.* The branchiostegal rays are squared off distally, as are those of both *A. calva* and *A. scutata.* Infraorbital 4, although posteroventrally incomplete, is clearly closer to that of *A. scutata* than *A. calva* in being relatively larger than infraorbital 5, and in the posterodorsal corner being squared off rather than acute as in *A. calva.* Infraorbital 5 resembles that of *A. scutata* in size relative to infraorbital 4, the anterior end being narrower than in *A. scutata;* this feature contributes to lessening the relative width of the orbit. The dentary resembles that of *A. scutata* in being wider anteriorly than in *A. calva;* the dorsal lingual surface only slightly overlaps the ventral lingual surface as in *A. scutata* (Fig. 18); Meckel's groove is thus similar to that of *A. scutata.* There is no available palate in *A. scutata* for comparison. The number of vomerine teeth is 18 and 21, which is bracketed by the range for *A. calva* (Estes and Berberian, 1969: 5). As Estes (1964) noted for this specimen, these teeth are sharper and more incurved externally than internally; this disparity is more distinct in this form than in the extant species. The hyomandibular, entopterygoid, ectopterygoid, dermopalatine, and premaxilla are poorly preserved, but appear to resemble these bones in *A. calva.*

Discussion

Estes (1964: 36) and Estes and Tihen (1964: 454) referred to this specimen as *Amia* sp. (and in error gave the source as White River Formation). The specimen resembles *A. scutata* in some elements, *A. calva* in others, and is intermediate in several character-states, notably bone thickness and size of orbits. It does, however, appear to show a stronger resemblance to *A. scutata* than to *A. calva,* particularly in

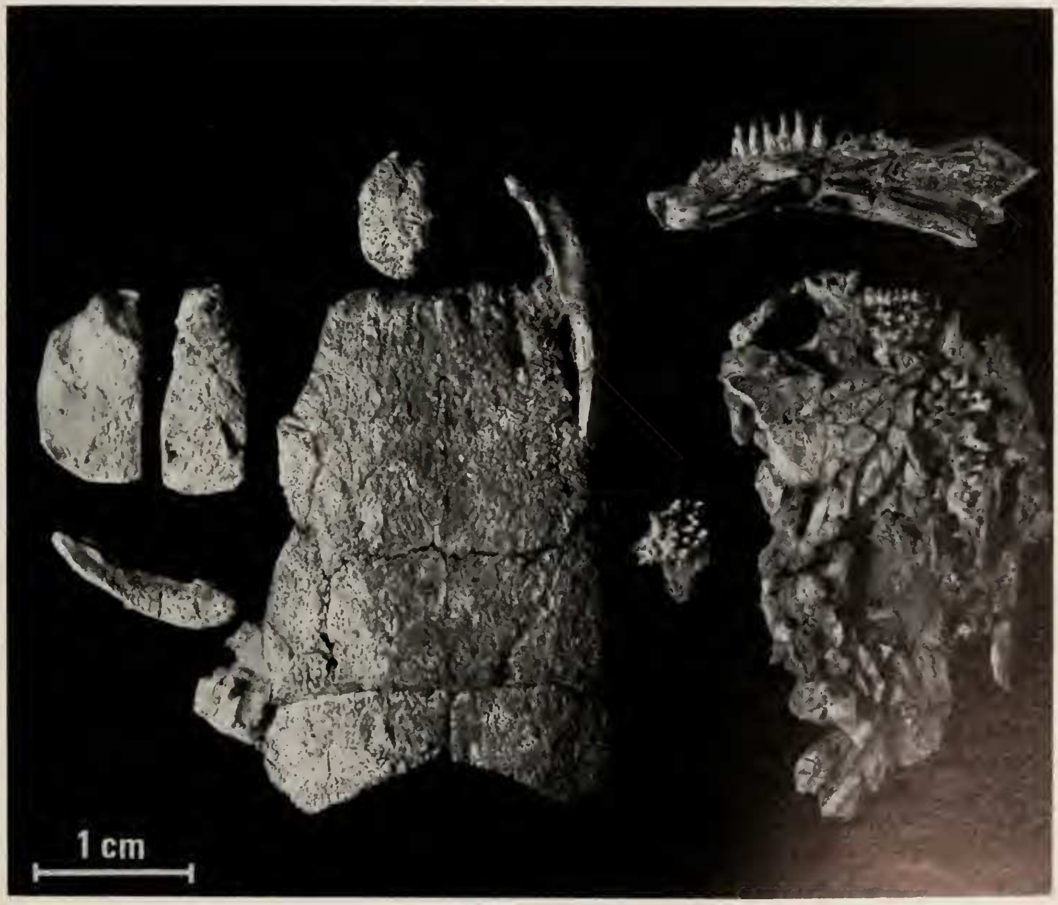

Fig. 29. *Amia* cf. *scutata* UC 38222, Late Miocene, Pawnee Creek Formation, Colorado.

the morphology of the extrascapular, pterotic, dentary, and infraorbitals 4 and 5, and I have thus compared it with the fossil species. Since this is a form that is both morphologically and temporally intermediate between *A. scutata* and *A. calva*, it is difficult to determine whether or not this specimen actually represents *A. scutata* or a later stage of evolution leading to *A. calva*, but it is at least of interest in documenting the slow phyletic development toward *A. calva* in mid-Cenozoic time.

Amia cf. *calva*

Hypodigm. PLIOCENE. Lower Valentine Formation, Nebraska: UCMP 65851, anterior portion of left dentary and a trunk vertebra; UMMP 52187, right nasal, ectopterygoid fragment, unidentified cranial fragments; UMMP 42185, right dentary fragment. Ogallala Formation, Kansas: UMMP 55574–55578, three right and two left dentary fragments; UMMP 55579, incomplete right cleithrum; UMMP 55583, a right extrascapular; UMMP 55580, a right maxilla; UMMP 55585, a left premaxilla; UMMP 55586, several scales.

Discussion

Smith (1962), and Estes and Tihen (1964) described as *Amia sp.* a nasal and dentary, and cranial fragments from the Lower Valentine Formation, Nebraska. Wilson (1968) described as *Amia calva* denatry fragments, a premaxilla, a maxilla, an extrascapular, an incomplete cleithrum, and several scales from the Ogallala Formation, Kansas. This Early Pliocene material resembles *A. calva* more closely than does the Miocene *A.* cf. *scutata* specimen noted above; the elements are very lightly ossified as in the Recent species. The cleithrum is distinctly *A. calva*-like in its lack of distal marginal dermal sculpture. The dentary fragments are also thinly ossified as in *A. calva,* but are slightly wider relative to the dentary in the Recent species, as in the Miocene form. Temporally, this Pliocene material is later than the Miocene form and earlier than *A. calva;* morphologically, however, the available elements conform with *A. calva.*

Amiidae *incertae sedis*

Hypodigm. CRETACEOUS. Paluxy Formation, Texas: SMUSMP 62270, dentary fragments, premaxillary fragment, vertebrae, maxillary fragments, and an unidentified palatal bone bearing teeth; FMNH 7050, basioccipital; FMNH 7051, mid-trunk vertebra; FMNH 7052, anterior trunk vertebra fragment; FMNH 7053–7054, anterior trunk vertebrae; FMNH 7055, caudal vertebra; FMNH 7056, small vertebrae; FMNH 7049, unidentified palatal bone bearing teeth.

Description

The dentaries are fragmentary (Fig. 30); the only diagnostic features available for comparison with other amiid forms are related to the anterior region of the dentary. The surfaces pits on the exterior side of the dentary are relatively larger and deeper than in any species of *Amia.* The dentaries lack the dorsal shelf adjacent to the lingual side of the alveolar ridge seen in *A. fragosa.* The coronoid articulation surface descends directly from the alveolar ridge, as in a *Urocles* dentary from the Late Jurassic (Purbeck) of England (BMNH 48236). The lingual surface above the Meckelian groove is relatively short, even more so than in *Amia uintaensis*, and the groove itself is quite wide, more so than in BMNH 48236. The anterior portions of the dentaries are relatively straight, rather than incurved as in *Amia fragosa,* and are evenly tapered to the symphyseal edge. The dentary and premaxilla teeth are broken, but in dorsal view the interior surfaces of the broken teeth are very even, lacking the serrated outline seen in other species of *Amia.* Only the anterior portion of the premaxilla is present; it bears nine alveoli, conforming in this respect with all *Amia* species. The premaxilla, although incomplete, displays the anterior (ventral) edge of the large foramen that is characteristic of *Amia.* Only part of the anterior maxilla is present in the specimens available, and since the more diagnostic aspects occur posteriorly, it is difficult to determine any affinities with particular species; the anterior portions that are available generally conform with those of *Amia.* The specific bones to which the palatal fragments belong cannot be identified. The smaller fragment (SMUSMP 62270) bears pillar-shaped teeth with nipple-like tips, as in the tooth-bearing palatal bones in species of *Amia.* Posterior to the spinal arterial foramina the basioccipital includes one fused vertebra. As in *Amia fragosa* and

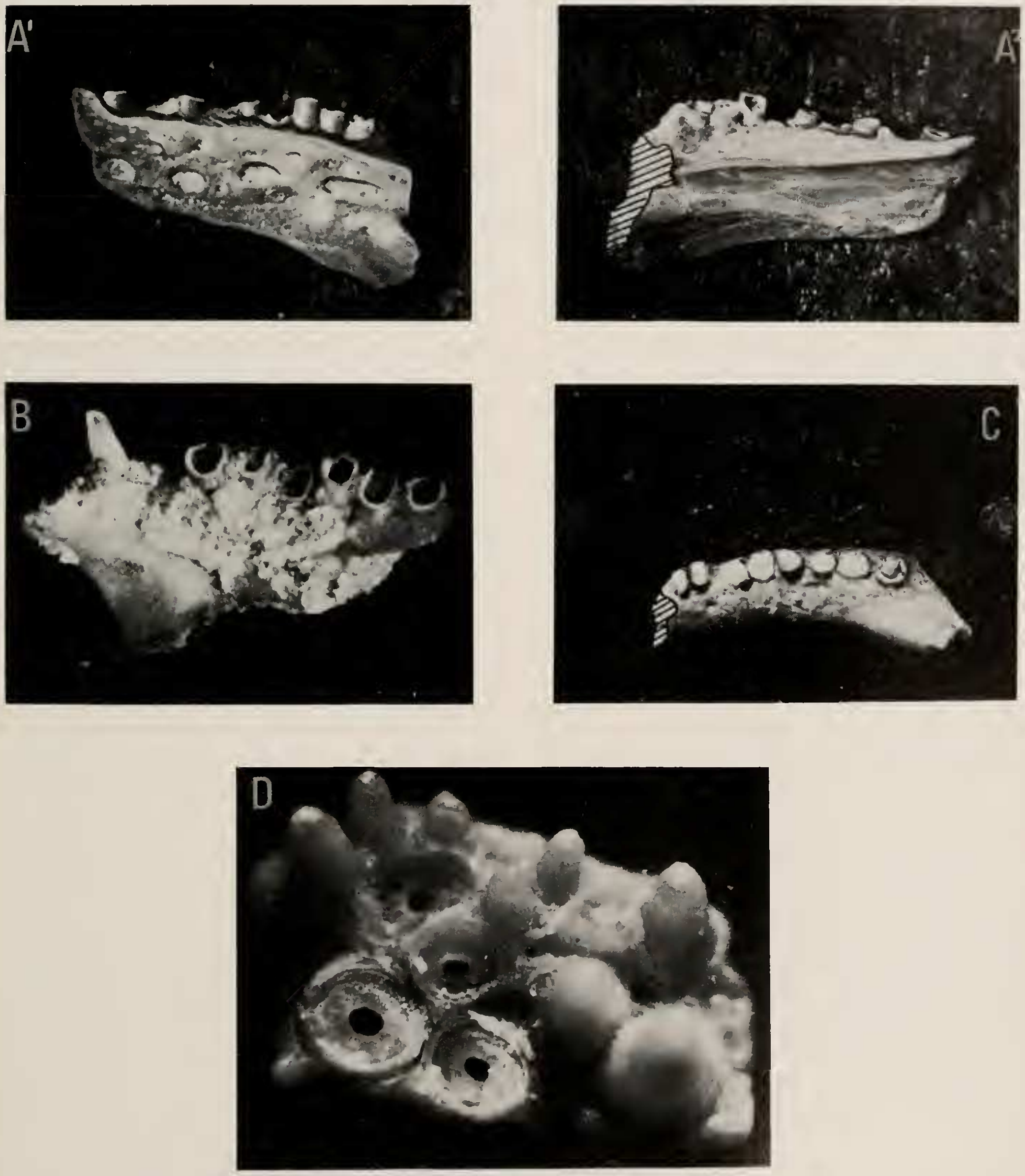

Fig. 30. Amiidae *incertae sedis,* Early Cretaceous, Paluxy Formation, Texas: A^1–A^2, anterior portion of left dentary; B, premaxillary fragment; C, anterior portion of right maxilla; D, unidentified palatal fragment. ×0.15

Amia calva, the basioccipital has an ovoid articular surface with no dorsal indentations between the neural facets. The large vertebrae are thickly ossified, as in the Cretaceous specimens of *Amia* cf. *uintaensis*. The chordal foramina are closed and the only available large mid-trunk centrum displays the pronounced triangular outline characteristic of *Amia uintaensis*. None of the large vertebrae display the characteristic *Amia* aortal facets; they do, however, possess neural facets, and the mid-trunk centra bear basapophyses. The small vertebrae are also thickly ossified and the chordal foramina of the trunk vertebrae are closed. As Traquair (1911: 39) noted for *Amiopsis dolloi*, the lateral sides of the vertebrae are marked by a number of variable excavations, or "oval fossae" (Fig. 7). These smaller mid-trunk vertebrae, unlike the large ones, display both aortal and neural facets, as well as basapophyses and lateral oval fossae.

Discussion

Thurmond (1969: 88) reported "various fragments of an undetermined amiid" from the Paluxy Formation of Texas, which is the earliest known occurrence of amiids in North America. He further noted that amiid material occurred both in freshwater and marine zones and that a further description of this material would be the subject of a later study. He was uncertain as to whether the amiids occurring in the marine zones were actually marine or were freshwater forms secondarily deposited in the marine areas. None of the material can be referred to *Amia* since it displays characteristics of *Amia uintaensis, Amia fragosa, Urocles*, and *Amiopsis*, as noted in the above description. The vertebrae suggest the possibility of more than one form: the large vertebrae are subtriangular and resemble *Amia uintaensis* in morphology, with the exception of the lack of aortal facets on the trunk vertebrae. The small vertebrae are *Amia fragosa*-like in morphology; they possess aortal facets, but also display lateral oval fossae characteristic of *Amiopsis*. In reviewing the European Jurassic and Cretaceous *Urocles*, Lange (1968) found little morphological justification to warrant continued generic distinction between *Urocles* and species described by Woodward (1916) as belonging to *Amiopsis* from the Purbeck Beds near Weymouth, Dorset. Lack of knowledge of the skull of *Amiopsis* makes it impossible to compare cranial elements with those of other amiids; the singular postcranial feature characterizing *Amiopsis* is the lateral oval fossae of the vertebrae. Although Lange suggests that both *Amiopsis* and *Amia* evolved independently from different *Urocles* species-groups, it is premature to attempt to do more than indicate morphological similarities or dissimilarities since the phylogenetic relationship of *Amiopsis* with *Urocles* or *Amia* cannot be clearly defined until a much-needed review of the taxon has been completed, and until more *Amiopsis* material is made available for study.

The Paluxy material shows resemblances to two early *Amia* species, *Amia uintaensis* and *Amia fragosa*, as well as to the Late Mesozoic European amiids, *Urocles* and *Amiopsis*. Whether the Paluxy material represents one or more forms intermediate between *Amia* and *Urocles* (or *Amiopsis*) or whether it belongs to some other group of amiids that became extinct before the end of the Cretaceous cannot be determined, since taxonomic evaluation of this material is limited by the lack of articulated specimens.

SPECIMENS REMOVED FROM THE AMIIDAE

Miller (1968: 468–470, pl. 1, figs. 1, 3, 7–9) questionably identified as *Protamia* sp. one large (FHKSCM 13025) and three small centra (FHKSCM 13024–9) recovered from a channel sandstone cut into the Upper Cretaceous Black Creek Formation, Phoebus Landing, North Carolina. Since all known *Amia* are freshwater forms and since these centra were associated with various marine vertebrates, Miller (1968: 467) concluded that the channel sandstone contained a mixed fauna, "the channel sandstone formed in an estuarine or tidal environment."

My studies indicate that these specimens are not amiid. The smaller vertebrae are horizontally ovoid. *A. uintaensis* trunk centra have concavities between the basapophyses and aortal facets (Fig. 26, A–C). A thin section (Fig. 26, G) through the articular surface of one of the North Carolina specimens (FHKSCM 13924–9) has a radial structure resembling that of *Squatina* and other sharks (Hasse, 1882, tables 17–18). All layers are laminated parallel to the exterior surface and are crossed by various perpendicular vascular foramina. Their articular surfaces are slightly concave, while those of *Amia* are markedly so. Each of the small vertebrae bear horizontal basapophyses as in Recent *Squalus,* and are best referred to the elasmobranchs.

The large vertebra is a cetacean caudal (Fig. 26, H), possibly belonging to the Cetotheriidae (Clayton Ray, 1971, personal communication). The centrum is ovoid, with very slightly concave articular surfaces, and lacks a chordal foramen, as well as ventral facets. The dorsal facets for the accommodation of metapophyses are well defined. Since this centrum is from a marine mammal, it is more probably from the Miocene (Calvert Formation?) than from the Cretaceous Black Creek Formation.

Eastman (1899) described *Amiopsis dartoni* from a partial opercular series, pectoral fin, and associated cycloid scales from the Late Jurassic marine Sundance Formation, South Dakota. Eastman felt that the many "stout ribs" associated with the pectoral fin suggested a well-ossified *Amia*-like vertebral column and the semicircular operculum conformed with that of *A. calva.* Since the scales are covered superficially with ganoine and appear elliptical, Eastman placed this form among the Amiidae. He allocated the generic name, *Amiopsis,* on a temporal basis. According to Bobb Schaeffer, (1971, personal communication) the holotype (USNM 4792) and the paratypes (MCZ 9696, USNM 4793) are to be tentatively referred to the Leptolepidae on the basis of morphology of opercular series and pectoral fin lepidotrichia. Schaeffer is currently studying the Late Jurassic North American fishes and is including a more extensive discussion of this material in his review.

SUMMARY AND CONCLUSIONS

This survey of the osteology, morphometrics, and meristics of the North American fossil amiids indicates that the extant and fossil forms fall into four groups worthy of specific status: (1) *Amia fragosa,* (2) *A. uintaensis,* (3) *A. scutata,* and (4) *A. calva.* All these forms, excepting *A. fragosa,* have somewhat elongated bodies (approximately 85 centra) and sharp, conical coronoid and palatal teeth. Although the coronoid and palatal teeth of *A. uintaensis* are more sharply curved inwardly, the teeth are closer in morphology to those of *A. scutata* and *A. calva* than to the styliform teeth of *A. fragosa. A. uintaensis, A. fragosa,* and *A. scutata* all have a larger infraorbital 4 than infraorbital 5, greater degree of ossification of cranial elements, deeper orbital notch in the frontal, greater head/standard-length, and generally larger parietal/frontal ratio. These character-states clearly set the fossil species of *Amia* apart from the Recent *A. calva.*

Articulated specimens have yielded more information on the osteology of *A. fragosa. A. fragosa* is a short-bodied form (approximately 65 centra) with a smaller number of caudal lepidotrichia than in the other species of *Amia,* styliform palatal and coronoid teeth, deeper orbital excavation in the frontals, square parietals, and a short box-like skull having relatively short mandibles that occupy about half the head-length. The styliform crushing palatal teeth of *A. fragosa* suggest a durophagous habit, rather than the more predaceous habit indicated by the sharp palatal teeth of *A. uintaensis, A. scutata,* and *A. calva.* Although it is known that *A. calva* includes molluscs and crustaceans in its diet, perhaps *A. fragosa* was more exclusively adapted for shell crushing than the Recent species.

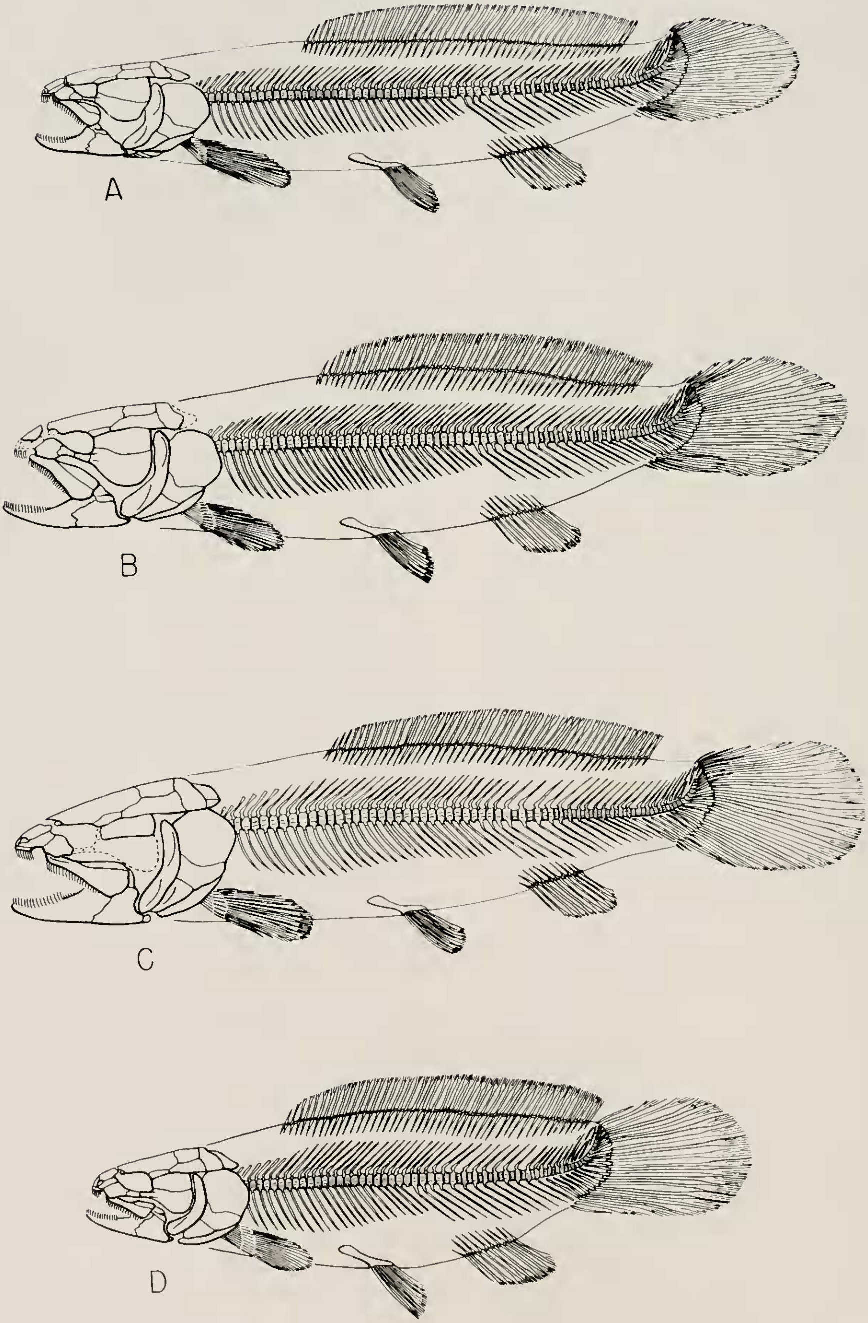

Fig. 31. Skull and body structure of A, *Amia calva;* B, *A. scutata;* C, *A. uintaensis;* and D, *A. fragosa.*

			Amia calva	*Amia cf. calva*	*Amia cf. scutata*	*Amia scutata*	*Amia uintaensis*	*Amia cf. uintaensis*	*Amia fragosa*	*Amiidae incertae sedis*	*Amia sp.*
PLEISTOCENE	POST-BLANCAN		X								
	BLANCAN										
PLIOCENE	HEMPHILLIAN	FOSSIL LAKE BEDS (IDAHO FM.)		X							
	CLARENDONIAN	WAKEENEY l.f. (OGALLALA FM.)		X							
		LOWER VALENTINE FM.		X							
MIOCENE	BARSTOVIAN	EUBANKS l.f. (PAWNEE CREEK FM.)			X						
	HEMINGFORDIAN										
	ARIKAREEAN	TURTLE BUTTE FM.									X
OLIGOCENE	WHITNEYAN	RUBY PAPER SHALE (PASSAMARI FM.)									X
	ORELLAN	GRANT HORSE PRAIRIE SHALE									X
		FLORISSANT FM.				X					
		ORELLA MEMBER (BRULE FM.)				X					
	CHADRONIAN	CHADRON FM.				X					
		CYPRESS HILLS FM.				X	X				
EOCENE	DUCHESNEAN	CLARNO FM.									X
		HORSEFLY RIVER BEDS									X
	UINTAN	UINTA FM.					X				
		WASHAKIE FM.					X				
	BRIDGERIAN	BRIDGER FM.					X		X		
	WASATCHIAN	WIND RIVER FM.					X				
		FOSSIL LAKE BEDS (GREEN RIVER FM.)					X		X		
		GOLDEN VALLEY FM.					X		X		
		WASATCH FM.					X		X		
		GRAYBULL BEDS (WILLWOOD FM.)					X		X		
PALEOCENE	CLARKFORKIAN	BEAR CREEK l.f. (FORT UNION FM.)					X				
		SILVER COULEE l.f. (FORT UNION FM.)							X		
	TIFFANIAN	MELVILLE FM.							X		
		SAUNDERS CREEK l.f. (PASKAPOO FM.)					X		X		
		CEDAR POINT QUARRY l.f. (FORT UNION FM)							X		
	TORREJONIAN	MEDICINE ROCKS l.f. (TONGUE RIVER FM.)					X		X		
		ROCK BENCH l.f. (FORT UNION FM.)							X		
	PUERCAN	TULLOCK FM.							X		
		MANTUA l.f (FORT UNION FM.)						?X	X		
CRETACEOUS	MAASTRICHTIAN	HELL CREEK FM.						X	X		
		LANCE FM.						X	X		
		OJO ALAMO FM.						X			
		AGUJA FM.						X			
		EDMONTON FM.							X		
	CAMPANIAN	JUDITH RIVER FM.							X		
		"MESAVERDE" FM.							X		
		OLDMAN FM.							X		
	ALBIAN	BUTLER FARM l.f. (PALUXY FM.)								X	

Table 18. Major deposits containing remains of *Amia* in the western interior of the United States and Canada

Seven genera and twenty-three amiid species (Table 19) have been described in the literature. Estes (1964) synonymized *Stylomyleodon lacus* with *Kindleia fragosa,* and Estes and Berberian (1969) referred the genus *Kindleia* to *Amia,* thereby confirming the suggestion of Janot (1969). *Paramiatus gurleyi* (Romer and Fryxell, 1928) is unquestionably a synonym of *A. fragosa.* Regardless of possible synonymy with European taxa, the stratigraphic range of *A. fragosa* is remarkably long, extending as it does from the Late Cretaceous through the Middle Eocene. Although *A. fragosa* is better known than the other fossil species, and was extensively described by Estes (1964), O'Brien (1969), and Estes and Berberian (1969), its phylogenetic relationship to them and to *A. calva* could not be understood without comparative information on both the other fossil forms and *A. calva* (Fig. 32).

A. newberrianus and *A. depressus* (Marsh, 1871), and *A. gracilis* (Leidy, 1873a), described from undiagnostic vertebral characters, are considered here as *nomina dubia.*

A. uintaensis is a form having a relatively greater body-length than the other species of *Amia.* It has approximately the same total number of vertebrae as *A. calva* and *A. scutata,* but the arrangement of the column varies meristically from them. Its head is more elongated than that of the other forms, with the jaws occupying over two-thirds of the head-length. The vomerine teeth are sharp (as are the palatal and coronoid teeth), as they are in *A. scutata* and *A. calva,* but are more than twice as numerous as in these later forms. The present study confirms the opinions of Romer and Fryxell (1928), Estes (1964), and Estes and Berberian (1969) that the differences between *Amia* and *Protamia, Hypamia,* and *Pappichthys* are insufficient for the recognition of any of the latter as genera distinct from *Amia. Hypamia elegans* (Leidy, 1873a) is considered a *nomen dubium,* being based on vertebral characters that cannot be distinguished from those of the other species. *Protamia media* (Leidy, 1873a), *Pappichthys symphysis, P. corsonii, P. medius, P. plicatus, P. sclerops, P. laevis* (all described by Cope, 1873), as well as *Amia macrospondyla* and *A. whiteavesiana* (Cope, 1891), are all considered here as synonyms of *A. uintaensis;* they were based on undiagnostic vertebral characters and morphology of the skull elements. Material of large amiids from the Late Cretaceous Lance and Hell Creek formations is referred to *A.* cf. *uintaensis,* since the material differs only in minor respects from the Paleocene and Eocene specimens. It cannot be determined whether this material represents actual populations of *A. uintaensis* or an earlier stage of its evolution. The stratigraphic range of *A. uintaensis* extends from the Paleocene to the Early Oligocene.

A. scutata, an Early to Middle Oligocene long-bodied form, shares cranial characters with both *A. uintaensis* and *A. calva.* Although it has closer morphometric and meristic affinities to the Recent form, it is structually and temporally intermediate between *A. uintaensis* and *A. calva;* it resembles the more primitive *A. uintaensis* in the morphology of Meckel's groove and coronoid articulation surface of the dentary, greater ossification, and in having an elongated skull with a greater head/standard-length than in *A. calva. A. dictyocephala* (Cope, 1875) is considered a synonym of *A. scutata;* it was based on undiagnostic meristic characters. In the evolutionary continuum, *A. scutata* appears to be an intermediate stage between *A. uintaensis* and *A. calva* (Fig. 32). A more direct line of evolution exists between *A. scutata* and *A. calva;* this is supported by Miocene and Pliocene amiid material that displays cranial elements closely transitional between the two species. Thus the Recent species of *A. calva* had begun at least by the beginning of the Pliocene, and *A. calva* was apparently distinct from *A. scutata* by that time. It appears that *A. fragosa* represents an amiid population that survived until the Middle or Late Eocene and had no phylogenetic affinities with the modern form beyond this time.

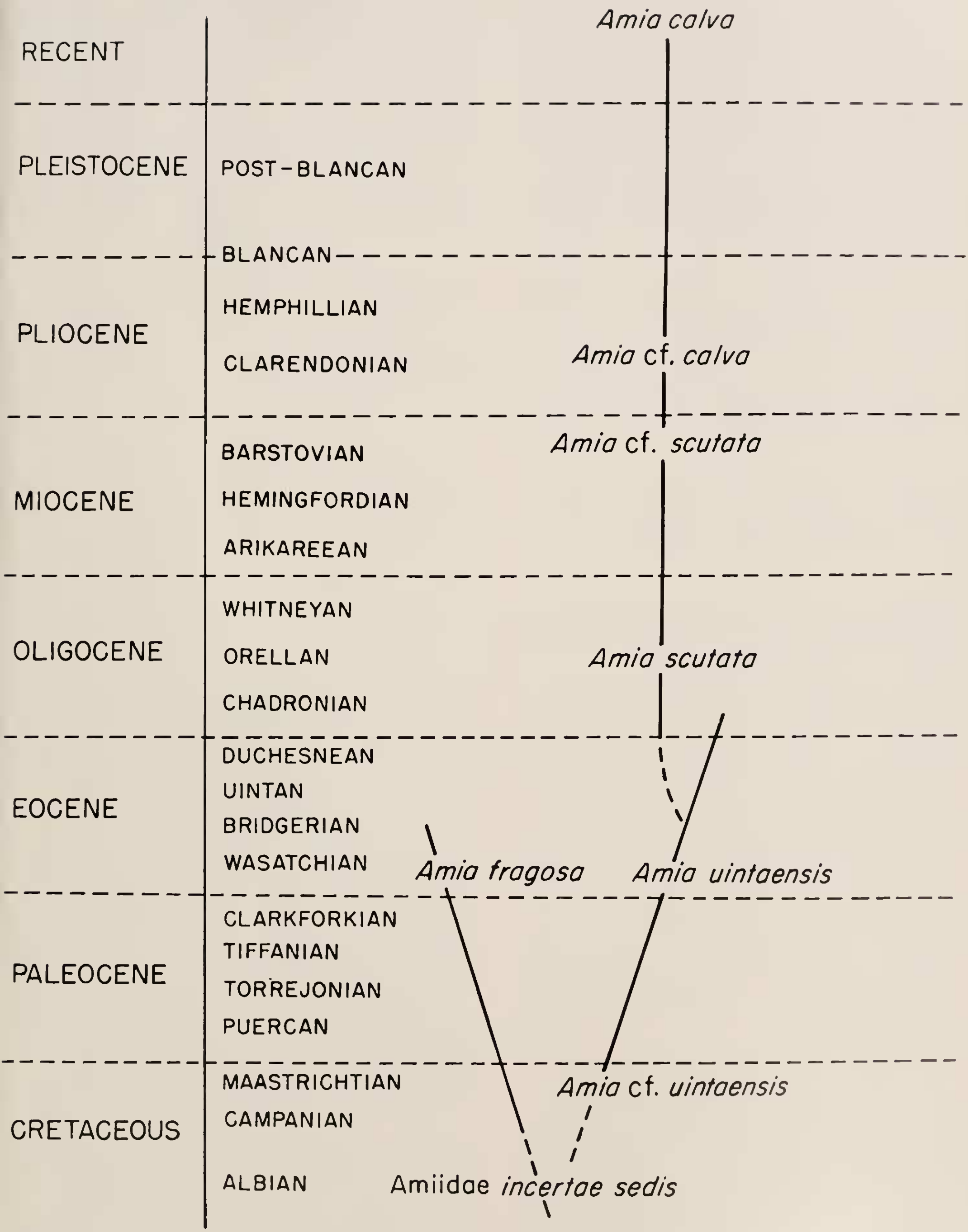

Fig. 32. Suggested phylogenetic relationships within the genus *Amia*.

In the North American fossil record, fossil remains unquestionably those of the family Amiidae first occur in the Lower Cretaceous (Albian) sediments of Texas. However, none of the material can be referred to any known species of *Amia;* it displays character-states resembling those of *Amia uintaensis* and *Amia fragosa,* as well as the European *Urocles.* Some of the vertebrae resemble those of *Amiopsis.* The Paluxy material may represent either one or more forms transitional between *Amia* and the Late Mesozoic European *Urocles* (or *Amiopsis*), or an as yet undescribed line. The body-length of *Amia fragosa* appears to be a primitive feature derived from the earlier amiids *Urocles, Sinamia, Ikechaoamia,* and *Amiopsis.* Despite their different vertebral columns, *Amia fragosa* and *A. uintaensis* show similar morphology of the cranial elements, but the nature of the probable common origin of these forms is still uncertain in the absence of a more complete fossil record.

Remains of amiids referable to or close to *Amia fragosa* and *A. uintaensis* have been described from the Paleocene, Eocene, and Oligocene of Europe, and the Eocene of Asia. Additional but still not definitive evidence supports Estes' (1964) and Estes and Berberian's (1969) suggested synonymy of *A. russelli* (Late Paleocene, France), *A. kehreri* (Middle Eocene, Germany), and *A. munieri* (Early Oligocene, France) with *A. fragosa. Pseudamia heintzi* (Eocene, Spitzbergen) and *A. valenciennesi* (Eocene, France) are also possible synonyms of *A. fragosa. A. valenciennesi* is the oldest name and would take precedence over *A. fragosa.* Cranial similarities confirm the synonymy of *A. robusta* (Late Paleocene, France) with *A. uintaensis.*

European and North American fossil *Amia* occurred in freshwater deposits and apparently occupied a habitat much like that of the Recent species. According to Westoll (1965: 19–20) the distribution of freshwater vertebrates is a useful indication of "direct continental communication," since ". . . descendents of a common stock on different modern continents must have used essentially a terrestial route." The present study further amplifies similarities in the Paleocene and Early Eocene amiid fossil record of North America and Europe. This distribution of amiids adds to the similarity of assemblages of Paleocene and Early Eocene lower vertebrates (Estes *et al.,* 1967) and mammals (McKenna, 1972) on the two continents. The occurrence of *Pseudamia heintzi* in the Eocene deposits of Spitzbergen may be additional evidence for the existence of the De Geer migration route (bridging Europe, Spitzbergen, and North America during the Paleocene and until the close of Sparnacian time), especially if suggested relationship to *A. fragosa* could be demonstrated. The Asian form *A. mongoliensis* resembles *A. uintaensis* in minor respects but is sufficiently distinct in itself to be maintained as a separate species.

TABLE 19. AMIID GENERA AND SPECIES OF VARIOUS AUTHORS DISCUSSED IN TEXT IN RELATION TO THE REVISED TAXONOMY

Amia calva	*Amia calva*
Kindleia fragosa	*Amia fragosa*
Stylomyleodon lacus	
Amia fragosa	
Paramiatus gurleyi	
Amia scutata	*Amia scutata*
Amia dictyocephala	
Amia exilis	
Protamia uintaensis	*Amia uintaensis*
Protamia media	
Pappichthys medius	
Pappichthys plicatus	
Pappichthys sclerops	
Pappichthys laevis	
Pappichthys symphysis	
Pappichthys corsonii	
Amia whiteavesiana	
Amia macrospondyla	
Amia depressus	*nomina dubia*
Amia newberrianus	
Amia gracilis	
Hypamia elegans	
Amia selwyniana	*nomen nudum*

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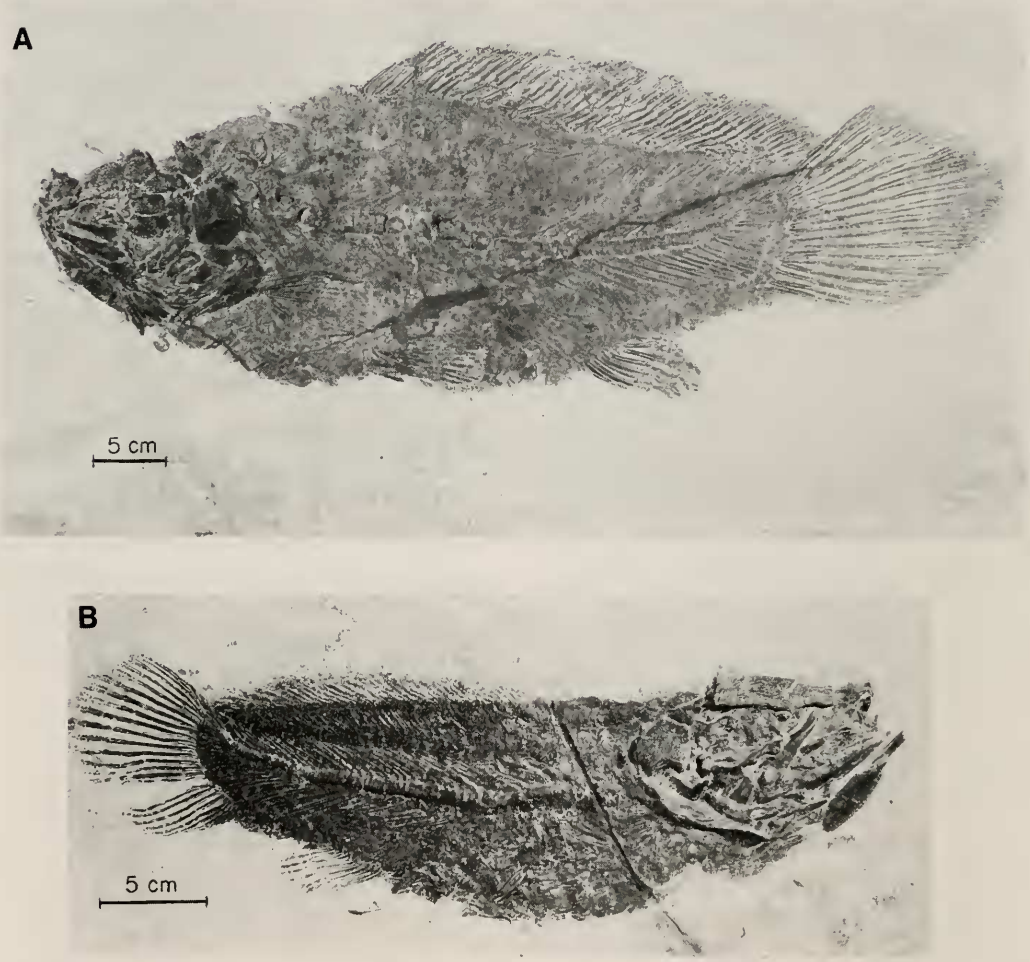

Plate 1. A, "*Paramiatus gurleyi*" FMNH 2201, Early Eocene, Green River Formation, Wyoming; B, *Amia fragosa* MCZ 5347, Early Eocene, Green River Formation, Wyoming.

Plate 2. *Amia kehreri* BMNH P33480, collected by Walter Kühne in 1951 from Middle Eocene deposits at Messel bei Darmstadt.

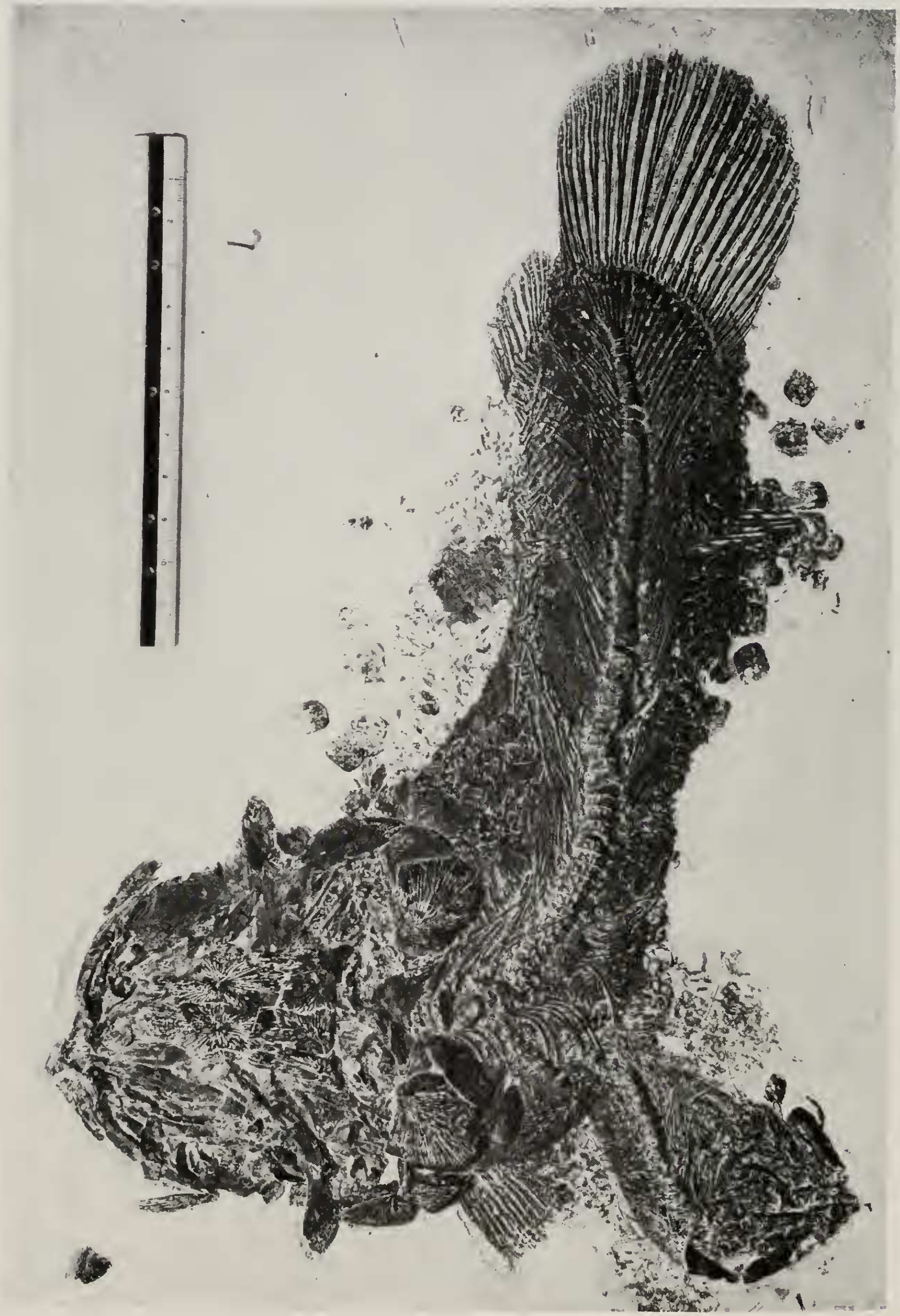

Plate 3. *Amia uintaensis* PU 13865, Early Eocene, Green River Formation, Wyoming.

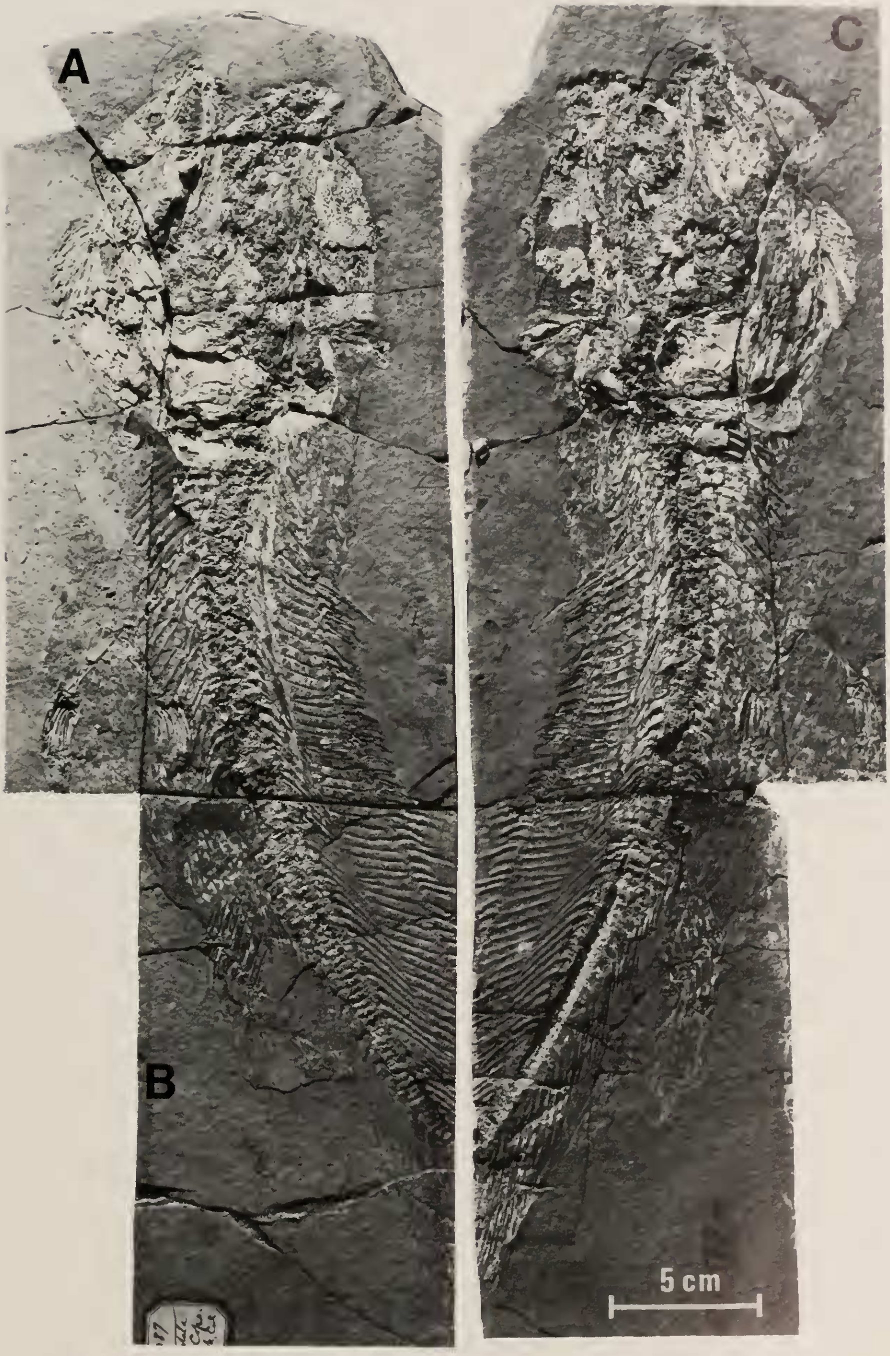

Plate 4. *Amia scutata*, Middle Oligocene, Florissant Formation, Colorado: A, counterpart YPM 6243; B, counterpart USNM 4087; C, PU 10172.